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A new stereotaxic coordinate system for the
rabbit's brain stem

The medial lemniscus of the rabbit; its
course through the brain stem and the
origin, fibre-content and termination
of its components

Bartolomeo Matricali

1961

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PROEFSCHRIFT TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE GENEESKUNDE AAN DE
RIJKSUNIVERSITEIT TE LEIDEN, OP GEZAG VAN
DE RECTOR MAGNIFICUS DR G. SEVENSTER, HOOG-
LERAAR IN DE FACULTEIT DER GODGELEERDHEID,
TEGEN DE BEDENKINGEN VAN DE FACULTEIT DER
GENEESKUNDE TE VERDEDIGEN OP WOENSDAG
11 OCTOBER 1961 TE 16 UUR

DOOR

BARTOLOMEO MATRICALI

GEBOREN TE LUCCA (ITALIË) IN 1932

Promotor: Prof. dr W. J. C. VERHAART

Aan Beb

A babbo e mamma

CONTENTS

A) A new stereotaxic coordinate system for the rabbit's brain stem	9
B) The medial lemniscus of the rabbit; its course through the brain stem and the origin, fibre-content and termination of its components	24
1) Samenvatting.	24
2) Introduction	26
3) Survey of the literature	27
4) Material and methods	29
5) The normal aspect of the medial lemniscus	30
6) Experimental material	34
a) The posterior funiculi components	34
b) The trigeminal component	43
c) Fibres derived from the cervical cord	48
d) Other components	52
7) Discussion	53
8) Summary	56
9) Riassunto	58
10) References	60

A) A NEW STEREOTAXIC COORDINATE SYSTEM FOR THE RABBIT'S BRAIN STEM.

When using the stereotaxic apparatus in neuro-anatomical experiments of the rabbit's brain stem, it is evident that sections will have to cut its long fibre systems more or less perpendicularly, because otherwise studying the fibre patterns is not feasible. This is of special importance when the fibre-staining method of HÄGGQVIST is employed.

HARRIS in 1937 developed an implement to fix the rabbit's head in the Horsley-Clark frame (fig. 1 and 2). With this head-holder SAWYER, EVERETT and GREEN in 1954 explored the diëncephalon of the rabbit.

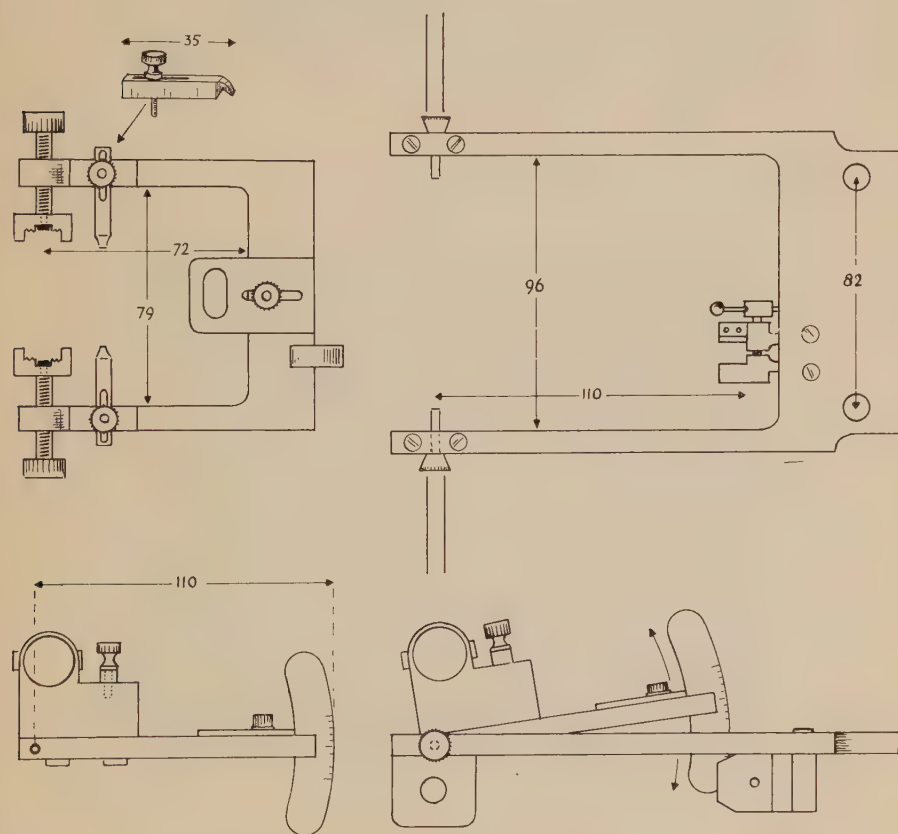


Fig. 1. The implement dismantled and provided with its dimensions.

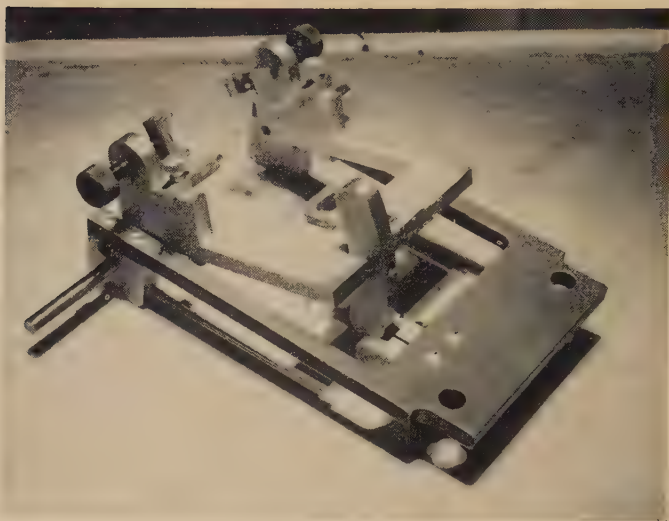


Fig. 2. The complete apparatus to be fixed in the Horsley-Clark frame.

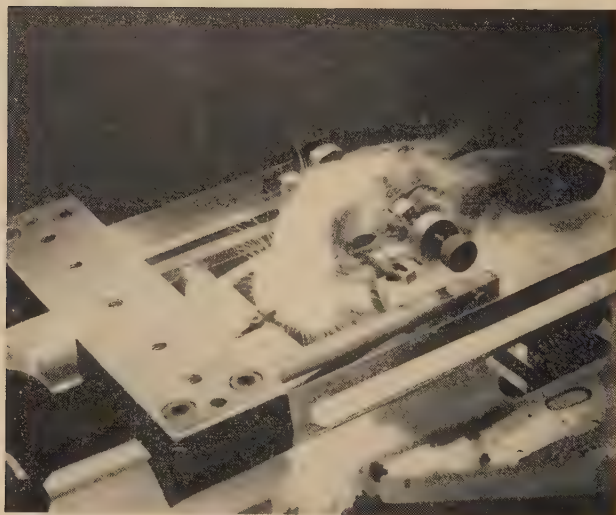


Fig. 3. A rabbit of the "Dutch breed" fixed in the headholder.

In this holder the skull is fixed at five points: the superior incisors in a slot, two bars on the lower orbital margins, and two clamps which fix the masseter muscles at the posterior part of the zygomaticus bone. The orbital fixation serves to keep the horizontal plane at its position and the others the sagittal plane. This implement allows the tilt of the longitudinal axis of the brain to be varied by turning the whole of the holder in the frame of the apparatus (fig. 3).

In the system of coordinates as used by SAWYER et al., however, the long fibre systems of the brain stem caudal to the di encephalon are not sectioned perpendicularly and therefore it is not appropriate for studies of this part of the C.N.S.. Therefore another system of coordinates was looked for and it could be developed by putting the base of the skull in a horizontal position by means of an X-ray picture (fig. 4). This showed that the base lies horizontally, when the bregma lay 4.2 mm ventral to the lambda suture. In order to be able to make pictures of the brain stem in which coordinates can be drawn, a certain breed of "Dutch rabbits" was used. The animals when weighing about 2.5 kg, were

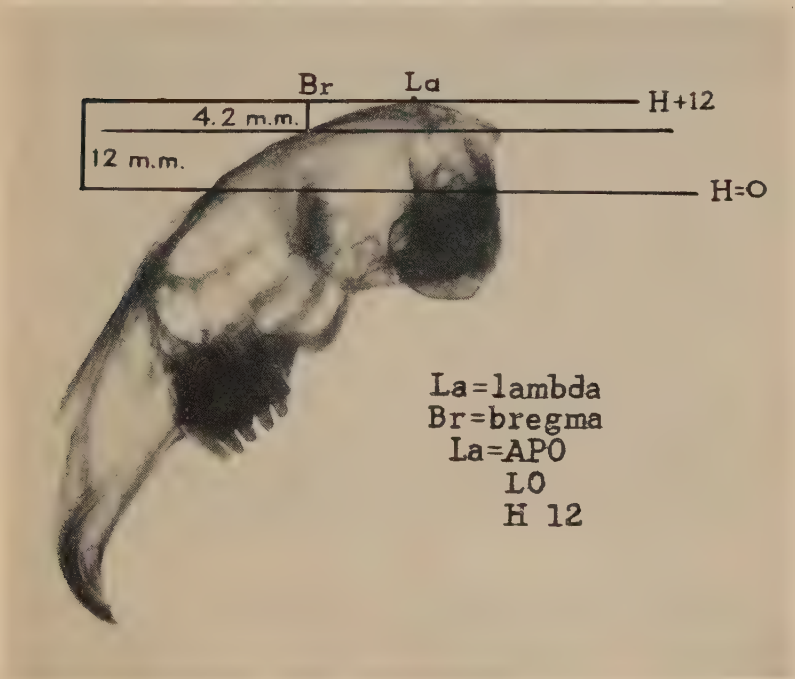


Fig. 4. An X-ray picture giving the horizontal planes and the tilt of the skull necessary for the right position of the base of the skull.

considered to be adult and proved to be quite uniform in size and shape of the skull.

Several of them, under deep urethane anesthesia, were put in the head-holder and the skull was fixed in the position described, with the bregma 4.2 mm below the lambda. In this position the lambda proved to be the most dorsal point of the skull and it was taken as the point of reference for the coordinates. The horizontal zero plane (H) was fixed 12 mm ventral to the lambda, just dorsal to the brain stem.

Both the sagittal and the antero-posterior zero planes similarly were fixed at this point. The animals were perfused with 10% formalin solution, the calvarium was opened and two steel wires were put through the C.N.S. in a horizontal plane. It proved to be necessary to rise the level of the wires by 1.4 mm to avoid unnecessary damaging and deforming the brain stem. From the transversal plane AoPo, through the lambda, both caudally and rostrally ink marks were made through the brain at every 3 mm distance in the vertical planes. Subsequently the brain was fixed in formalin and bichromate to be cut in transverse sections, parallel to the stereotaxic vertical planes. The stained sections of every corrected millimetre, corrected because of the shrinkage during fixation, dehydration and embedding, were photographed and pictured and the corrected coordinates both vertical and horizontal, were put at their proper sites, along the margin of the figures (fig. 5—fig. 15). The pictures show conspicuously that the long fibre systems are cut perpendicularly, which makes studying their fibre-content feasible.

When aiming at electrolytic destruction of certain centra or fibre-groups, the pictures and drawings can be used as a guide to localize the area to be coagulated at the experiments. The head is fixed in the holder in the way described, the skin over the skull is opened and the inner-frame of the holder tilted in the sagittal plane, till the bregma lies in a plane 4.2 mm below of the lambda. Then taking the lambda as the reference point, $H = 12$, $AP = 0$, $L = 0$, localizing the different elements of the brain stem is relatively easy.



Fig 5.



Fig. 6.

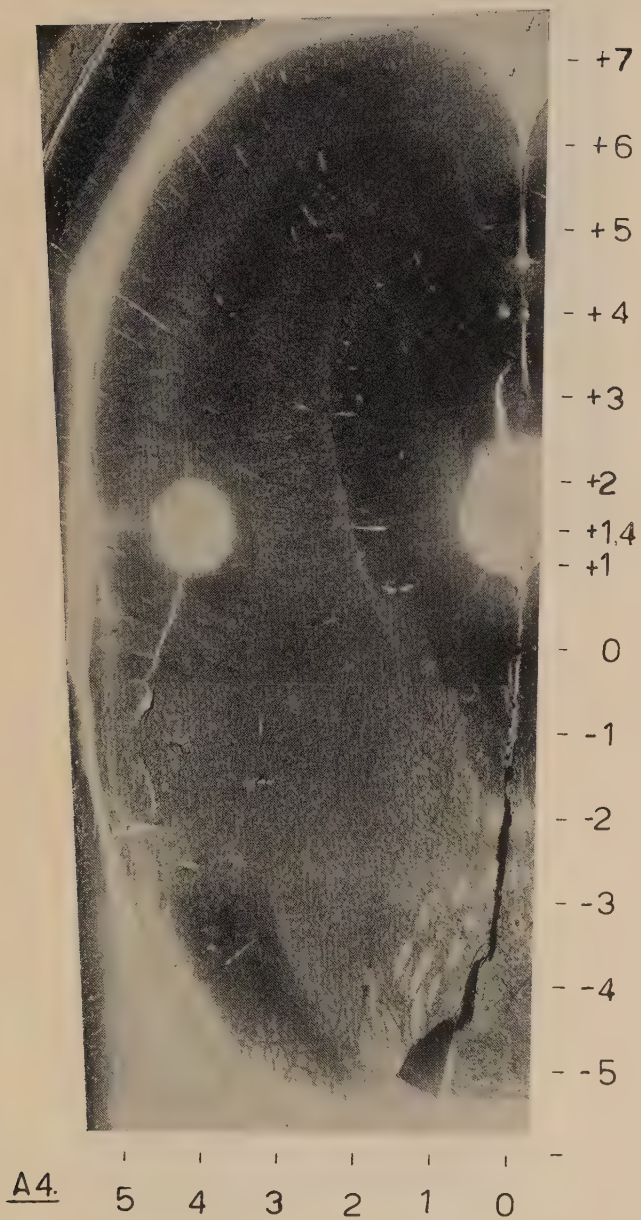


Fig. 7.

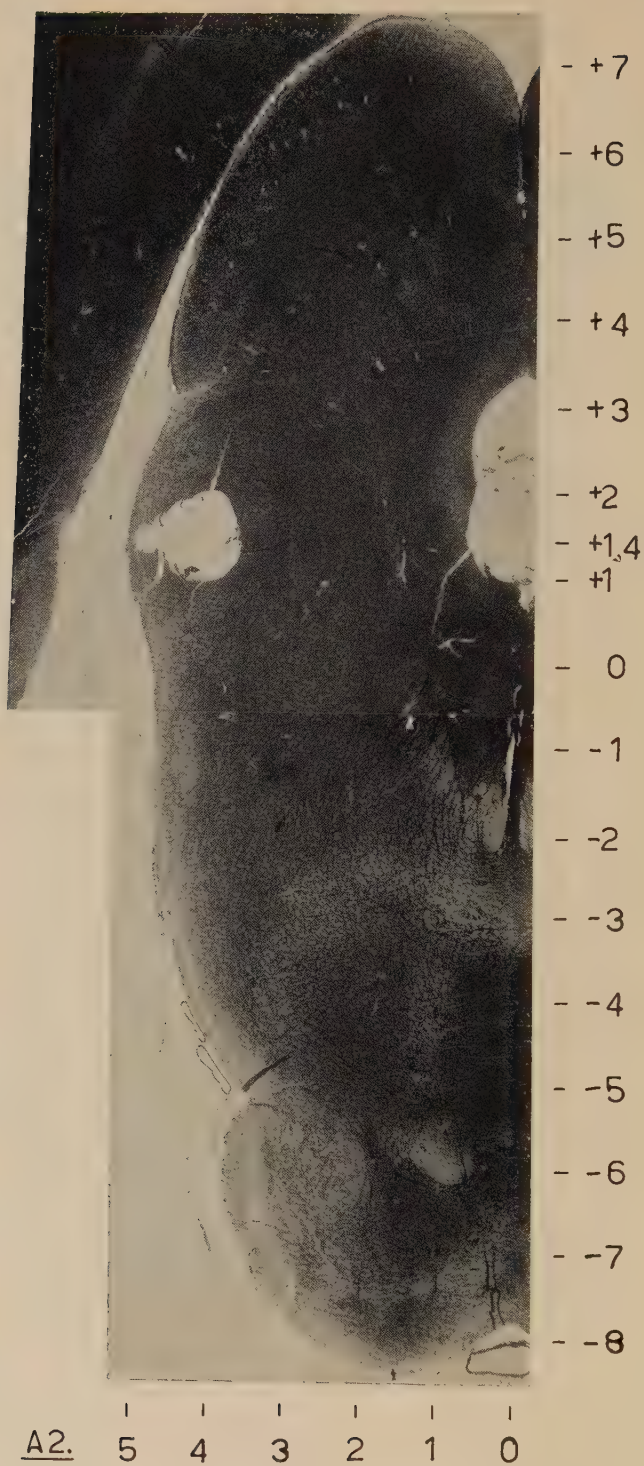


Fig. 8.



Fig. 9.

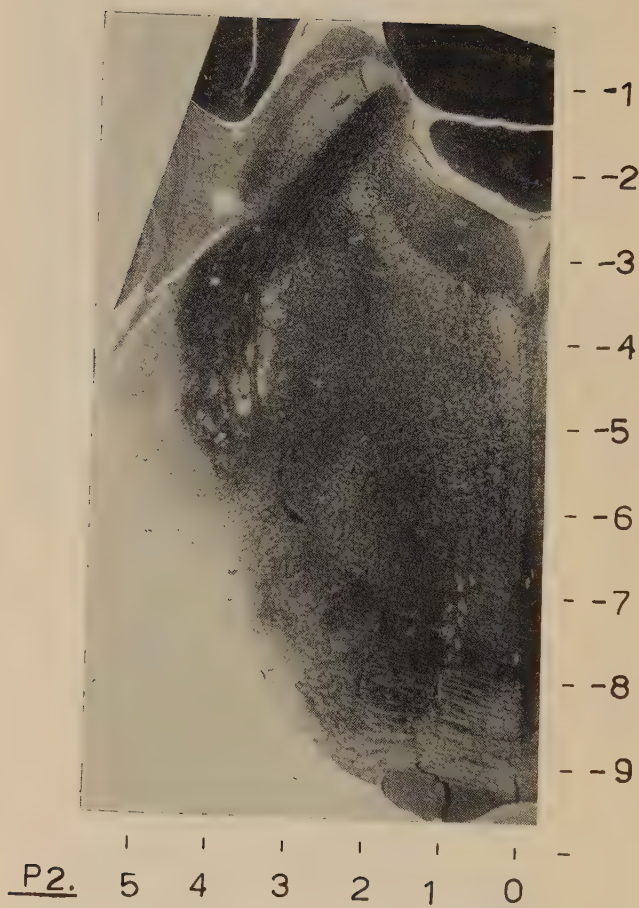


Fig. 10.

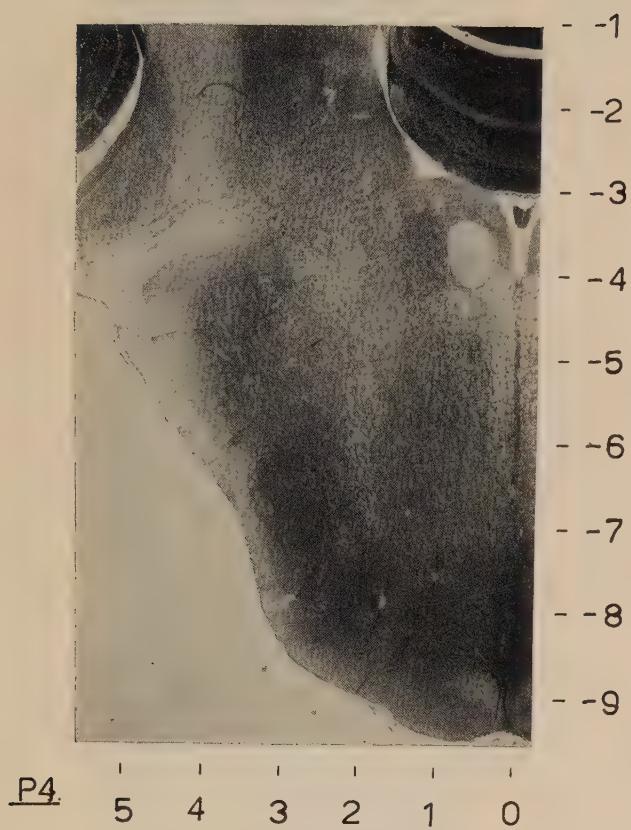


Fig. 11.

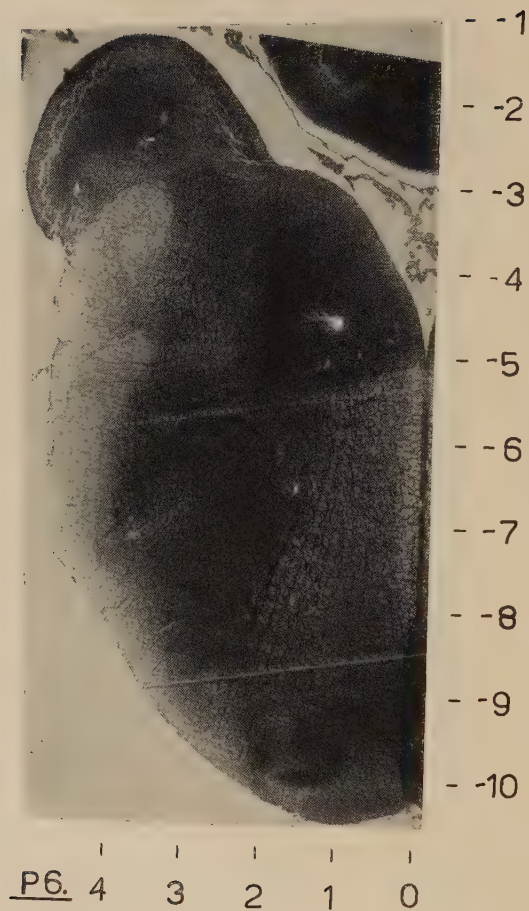


Fig. 12.

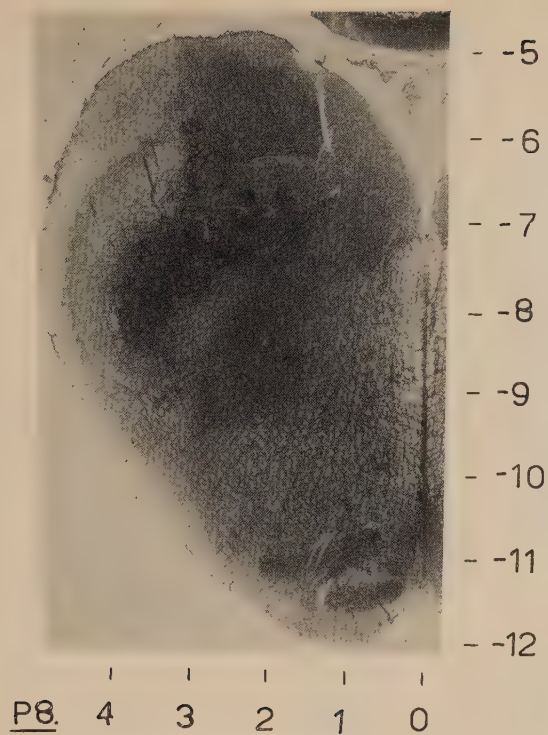


Fig. 13.

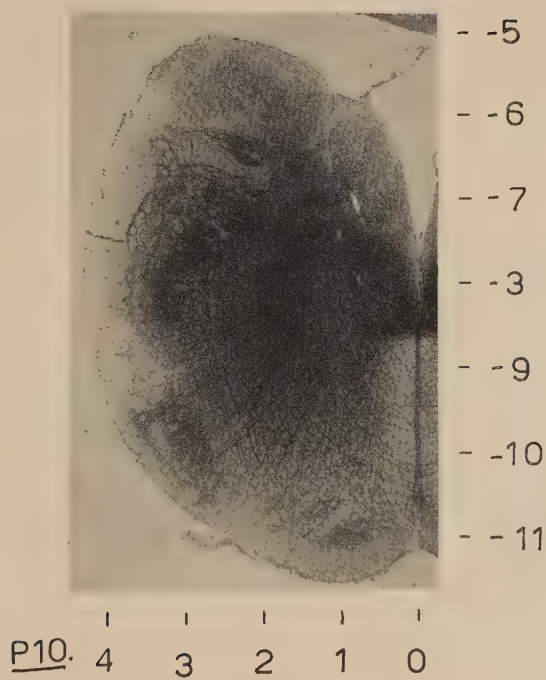


Fig. 14.

LIST OF ABBREVIATIONS.

A 8.	V.P.L.	Nc ventro-postero-lateralis.
	V.P.M.	Nc ventro-postero-medialis.
	V.L.	Nc ventro-lateralis.
	V.M.	Nc ventro-medialis.
	V.M.L.	lamina medullaris ventralis thalami.
	Op.T.	tractus opticus.
	P.C.	pedunculus cerebri.
	Sub.Th.	subthalamus.
A 4.	C.S.	colliculus superior.
	C.G.	griseum centrale.
	Nu III	Nc oculomotorius.
	F.L.M.	fasciculus longitudinalis medialis.
	Nu.R.	Nc ruber.
	N. III	Ne oculomotorius.
	S.N.	substantia nigra.
	L.M.	lemniscus medialis.
	I.P.N.	Nc interpeduncularis.
AOPO.	C.I.	colliculus inferior.
	L.L.	lemniscus lateralis.
	Br.Conj.	brachium conjunctivum.
	Br.P.	brachium pontis.
	Nu.L.L.	Nc lemnisci lateralis.
P 4.	C.R.	corpus restiforme.
	N. VIII	Ne octavus.
	R.Desc.N.V.	ramus descendens nervi quinti.
	Nu.Spin.Or.	Nc trigemini spinalis oralis.
	Sub.Ret.	substantia reticularis.
P 8.	Nu.Cun.Ext.	Nc cuneatus externus.
	Olv.Inf.	Oliva inferior.

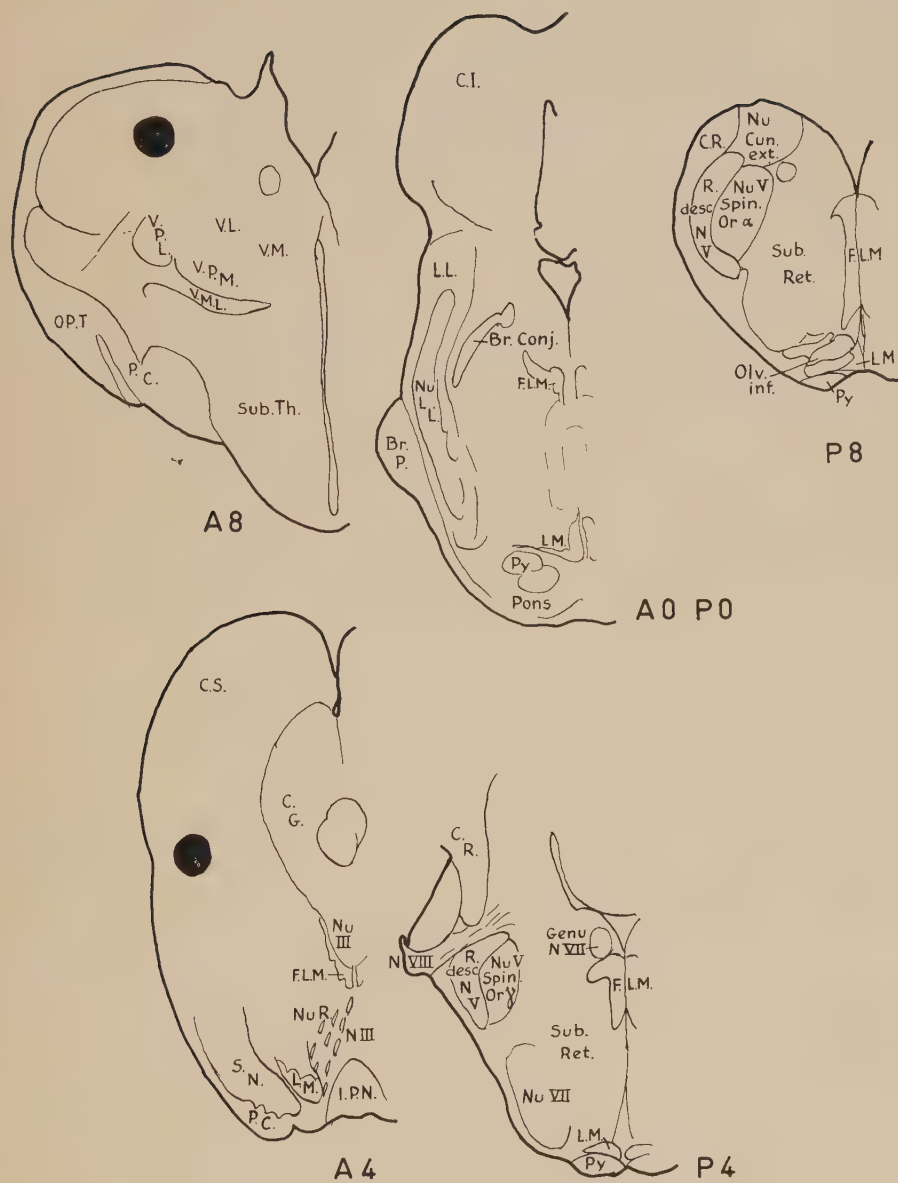


Fig. 15.

B) THE MEDIAL LEMNISCUS OF THE RABBIT; ITS COURSE THROUGH THE BRAIN STEM AND THE ORIGIN, FIBRE-CONTENT AND TERMINATION OF ITS COMPONENTS. AN EXPERIMENTAL STUDY.

1) SAMENVATTING.

Reeds in het normale Häggqvist preparaat is het mogelijk om verschillen te zien in het vezelpatroon, die optreden in het verloop van een baan. Deze verschillen in vezelsamenstelling waren duidelijk te vinden in de L.M. van het konijn. De eerste vezels, herkenbaar als L.M. vezels van dun en middeldik caliber, zijn reeds in het caudale niveau van de oliva inferior te vinden; tussen deze laatste, de raphe en de pyramide. Boven het niveau van de olijf zien we dat de L.M. steeds in mediale positie blijft liggen en 3 vezelgroepen van verschillend patroon bevat. In het ventrale deel zijn het vezels tot 2 micron, in het laterale gebied zijn er 2-5 micron-vezels bij en in het dorsale deel bovendien vezels tot 10 micron in diameter.

In het rostrale deel van het corpus trapezoides voegen grote hoeveelheden dunne vezels, kleiner dan 2 micron, zich mediaal bij de lemniscus. De oorspronkelijke component verplaatst zich daarbij naar lateraal en op hogere niveaus wordt het gehele mediale deel gevormd door deze nieuwe dunne vezels. In het mesencephalon liggen de oorspronkelijke vezels verspreid om deze dunne vezels heen. Van hier zijn de dunne vezels vervolgbaar naar de lamina medullaris ventralis van de thalamus en naar rostraal gaande onder het ventrale kerncomplex zien we deze lamina snel in omvang afnemen. Dit verschil in de vezelsamenstelling was duidelijk zichtbaar en vormde de aanleiding om deze componenten nader te identificeren.

Om oorsprong, verloop en eindigingen van deze verschillende onderdelen te analyseren zijn drie kleurmethodes toegepast: de Häggqvist en de Nauta-Gygax methode voor de gedegenerende vezels en de Nissl methode voor de retrograde celdegeneratie.

De achterstrengkern-component blijkt te ontstaan uit alle drie de kernen: de Nc gracilis, de Nc cuneatus internus en de Nc cuneatus externus, en in de contra-laterale L.M. gerangschikt te zijn, achtereenvolgens in het laterale gebied met vezels tot 5 micron, in het ventrale

gebied waar vezels tot 2 micron liggen en in het gehele dorsale gebied, waar zich vezels tot 10 micron in diameter bevinden.

Deze rangschikking gaat verloren ter hoogte van de pons, wanneer deze vezels zich naar lateraal verplaatsen. De vezels uit de Nc gracilis en de Nc cuneatus internus gaan het verst naar lateraal en een aantal lopen mee met de lemniscus lateralis naar de colliculus inferior waar ze eindigen. De overblijvende vezels uit de Nc gracilis en de Nc cuneatus internus en de vezels uit de Nc cuneatus externus rangschikken zich om de dunvezelige L.M. en lopen verspreid over een groot gebied naar het laterale deel van de lamina medullaris ventralis van de thalamus. De vezels die ventraal van de dunne vezels liggen, bereiken de lamina via een korte weg door de subthalamus. Deze vezels zien we massaal eindigen in de Nc V.P.L. van de thalamus; wanneer de Nc cuneatus externus gelaedeerd is, zien we ook enkele vezels in de Nc V.L..

Het dunvezelige deel dat zich boven het niveau van het corpus trapezoides bij de L.M. gaat voegen, blijkt uitsluitend afkomstig te zijn uit de contra-laterale Nc princeps van de N. trigeminus. Noch de pars oralis, noch de pars spinalis geven vezels naar de L.M.; ook bij lemniscus laesies werden er in deze kernen geen retrograde veranderingen gezien. Het meest caudale deel van de Nc princeps geeft in de contra-laterale L.M. de meest laterale vezels, het meest rostrale deel de meest mediale vezels. Deze rangschikking blijft gehandhaafd tot in de L.M.V. van de thalamus. Alle dunne trigeminus vezels hebben hun eindiging in de Nc arcuatus van de thalamus, die een veel grotere omvang heeft dan de Nc V.P.L., waar de achterstrengkernvezels eindigen.

De derde component van de L.M., bestaande uit vezels tot 2 micron in diameter, ontstaat reeds in het hoog-cervicale merg en is zelfs in het normale preparaat, even caudaal van de pyramide kruising, ventraal van de F.L.M. als een smalle band dunne vezels zichtbaar. In de L.M. liggen deze vezels lateraal en ventraal en naar rostraal toe gaande verplaatsen ze zich geheel naar lateraal in de L.M.. Deze vezels eindigen in het corpus geniculatum mediale. De oorsprong in de Nc cervicalis lateralis kon met retrograde celdegeneratie niet worden aangetoond, daar het verspreide cellen zijn, die geen goed omschreven kerngebied vormen.

Vezels uit andere kernen werden in de L.M. niet gevonden.

2) INTRODUCTION.

As has already been repeatedly pointed out (VAN BEUSEKOM, 1955; SIEPEK GIOK, 1956; BUSCH, 1961; and VOOGD, in print) Häggqvist's modification of the methylblue-eosin staining method of ALZHEIMER-MANN is very suitable for a study of the topography of the fibre systems in the central nervous system. This is especially so, because it demonstrates the axon and the myelinsheath of each separate fibre in contrasting colours and very often shows the ganglioncells with most of their dendrites as well. Moreover it exhibits Wallerian degeneration in both the axon and the myelinsheath from about 10 days after severance on. As in such cases it shows both the normal and the affected fibres, it is especially appropriate in localizing the severed fibrebundles between the normal. It however fails to show very fine solitary degenerated fibres, as well as the preterminal fibres in most of the grey centres. Therefore it has to be combined with one of the new silver-impregnation methods, in preference that of NAUTA and GYGAX as described in 1954. Because of this, most of the experiments were repeated, after the Häggqvist stained series had been studied, as will appear in the description of the experiments in the following chapters.

By showing the axons and myelinsheaths in contrasting colours Häggqvist's method exhibits the fibre-content of a tract clearly and, as was the case in this study, changes in fibre-content during the course in the brain stem in a certain tract are revealed almost at first sight. This was the first motive to the present study, as the inspection of a normal brain stem of the rabbit showed the medial lemniscus to change its fibre-content very much when ascending in the medulla and the pons.

3) SURVEY OF THE LITERATURE.

The medial lemniscus was described for the first time by REIL (1809) and later by VON BECHTEREW (1895). TSCHERMAK (1898) and PROBST (1902) stated that the fibres of the medial lemniscus (M.L.) have their origin in the nuclei gracilis and cuneatus.

Lamination in M.L. with regard to the components of different origin was looked for by several authors. VAN GEUCHTEN (1903) in the rabbit, FERRARO and BARRERA (1936) in the monkey, MATZKE (1949) and GLEES et al. (1951) in the cat, showed that all the fibres from the posterior funiculi nuclei cross and that the fibres from Goll's nucleus lie lateral to those from Burdach's nucleus. VERHAART (1954 and 1959) could confirm this and moreover demonstrated that the M.L. in different animals varies in localization. PROBST (1902) in the dog and FERRARO and BARRERA (1936) described fibres from the nucleus cuneatus externus to join the M.L..

The termination of the M.L. fibres in the cat (MATZKE 1951) and in macaca (BOWSER 1958) was found to be exclusively in the V.P.L. nucleus of the thalamus, one small bundle excepted which by way of the subthalamus reaches the L.M.V. thalami. Conformingly BERRY, KARL and HINSEY (1950) in physiological experiments in the cat and macaca found the efferents from the nuclei of Goll and Burdach to cross completely and to terminate exclusively in the V.P.L. nucleus of the thalamus. Terminations in the lower brain stem were not found.

Fibres in the M.L. originating from nuclei other than those of the posterior funiculi were found by WALLENBERG (1896 and 1905) in the rabbit, from the trigeminal complex and PROBST (1902) in the dog, from the descending nucleus of the trigeminal nerve. WALKER (1939) in the monkey and RUSSELL (1954) in the cat found fibres originating in the nuclei of the trigeminal nerve, both the main nucleus and that of the whole spinal part. VAN GEUCHTEN (1901) in the rabbit, LEWANDOWSKY (1904) and BUSCH (1961) in the cat found the origin only in the main sensory nucleus.

BERRY, ANDERSON and BROOKS (1956) in the cat studying the trigemino-thalamic pathways physiologically found the response in the M.L. following stimulation of the trigeminal nerve, always to be strictly crossed and present only rostral to the trapezoid body.

The termination of the secondary trigeminal pathway by MAGOUN and McKINLEY (1942), MOUNTCASTLE and HENNEMAN (1952) and by ROSE and MOUNTCASTLE (1952, 1960) unanimously was found to be the arcuate nucleus, with only some uncertain terminations in the centre median nucleus.

A component from the high-cervical cord was found by PROBST (1900) in the cat to lie in the lateral part of the M.L.. MORIN (1955) and CATALANO and LAMARSCHE (1957) could confirm this connexion in physiological experiments. BUSCH (1957) in the cat and MATRICALI (1957) in the rabbit could describe the course of these fibres originating in the two upper cervical segments, crossing with the pyramidal tract and taking their site in the lateral-dorsal part of the M.L. in which they proceed to the thalamus. BUSCH in the cat, with the method of retrograde celldegeneration could prove the fibres to originate at least partly in the nucleus cervicalis lateralis.

VON MONAKOW (1913), ALLEN (1932) and GEREBTZOFF (1939) described fibres of the solitary tract nucleus to join the M.L., but this could not be confirmed by other authors.

4) MATERIAL AND METHODS.

In this study, the rabbits used are adult animals of the "Dutch breed", weighing about 2.5 kg.

The lesions were made by electric coagulation on base of the stereotaxic atlas. Parts of the brain involved in the lesions were: the nuclei gracilis, cuneatus internus and cuneatus externus, the nuclei of the descending tract of the trigeminus over its whole length and the main sensory nucleus, the area of the nucleus of the tractus solitarius, the ventral part of the upper cervical cord and the M.L. itself.

The animals were divided into three groups, according to the length of their period of survival, depending on the staining method used.

The group intended for the Häggqvist staining method had a survival time of 21 days, the animals used for the retrograde celldegeneration only five days, because at this time the changes were as much distinct as possible, and the third group to be stained with the Nauta-Gygax silverimpregnation method was sacrificed 8 days after the operation.

Using these three staining methods, when comparing their results, it is readily feasible to get a good general view of the origin, composition, course and termination of the M.L..

5) THE NORMAL ASPECT OF THE MEDIAL LEMNISCUS.

The first fibres forming the M.L. are found next to the raphe, in the level of the most caudal part of the inferior olive. Proceeding to higher levels, in this area we see the number of the fibres increase considerably (fig. 16). They however do not shift to lateral, but keep their medial



Fig. 16. The M.L. at the rostral level of the inferior olive.

position. Along the raphe just rostral to the inferior olive, the fibres form a distinct tract. Looking at its pattern we can see that the fibre arrangement is not homogeneous over the whole surface area. With regard to their diameter the fibres can be divided into three groups: 0—2 micron, from 2—5 micron, and over 5 micron in diameter. In the ventral part the majority of the fibres are of the group from 1—2 micron in diameter. In the medio-dorsal part we find fibres of all sizes up to 2 micron, but also many fibres from 2—5 micron and over 5 micron up to 10 micron (fig. 17). In the lateral part fibres of both, the small and the large-sized fibre group are somewhat less in number.

This unhomogeneous arrangement of fibres is especially clear at the level of the trapezoid body. The whole M.L. keeps to the medial position along the raphe and is split up in bundles by the transverse fibres of the



Fig. 17. Rostral to the inferior olive, the differences in the fibre-pattern of the ventral and dorsal part are obvious.

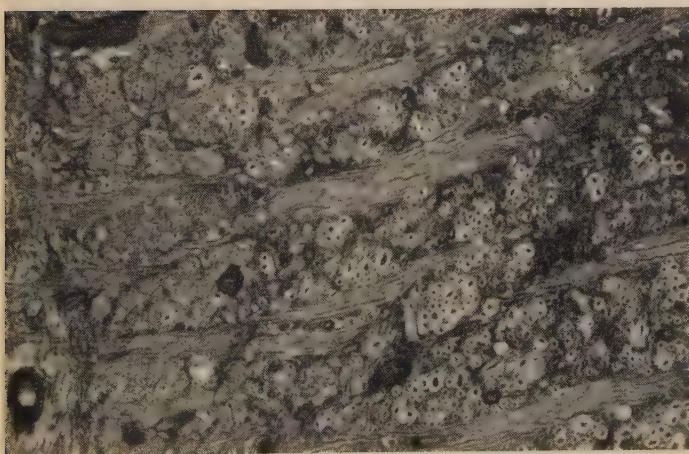


Fig. 18. At rostral trapezoid level and caudal pontine level, the thin-fibred component joins the M.L. in its medial part.

trapezoid body. At the level of the rostral end of the latter a new component of fibres takes its site in the medio-dorsal part of the M.L. (fig. 18). These fibres are smaller than 2 micron in diameter. They are enormous in quantity and fill about whole the M.L. in the higher levels. The fibres of more caudal origin are pushed laterally and subsequently constitute only a small portion of the M.L.. At the rostral part of the pons the whole M.L. from its medial position is pushed laterally and the lateral thick-fibred contingent intermingles with the medial thin-fibred component, in the intermedial part (fig. 19).

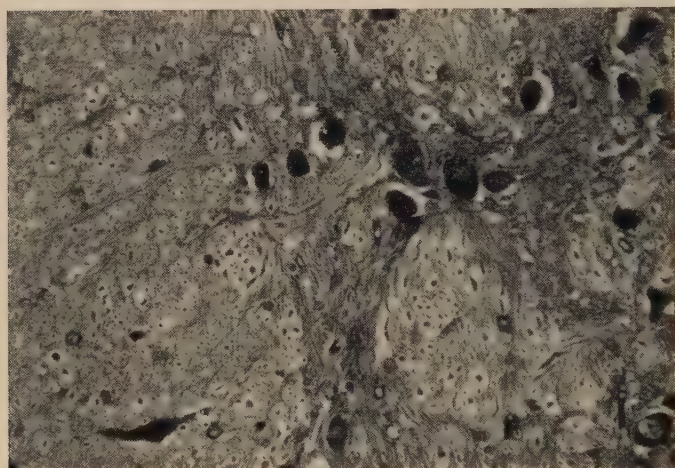


Fig. 19. The border between the thin and thick fibres at pontine levels.

In the mesencephalon the fibres of the M.L. move to dorsal and to lateral to form the lamina medullaris ventralis of the thalamus. In this lamina the distribution of fibres of different sizes is equal to that in the upper pontine levels. In the medial part we find the majority of the thin fibres (fig. 20), in the lateral part the thicker-fibred portion (fig. 21). In still more rostral levels we see that the fibres diminish in number while passing ventral to the ventro-posterior nuclei group of the thalamus.

In conclusion we can say that the first fibres composing the M.L. appear at the caudal level of the inferior olives, where they take their site along the raphe. Rostral to the inferior olives the M.L. fills a circumscribed surface area in which we can distinguish the unhomogeneous pattern. At the rostral end of the trapezoid body a great

number of thin fibres joins the M.L. in its medial-dorsal part, keeping the medial position in the near proximity of the raphe. In the mesencephalon when all the new fibres have reached the tract, the M.L. starts shifting to dorsal and lateral to form the lamina medullaris ventralis of the thalamus.

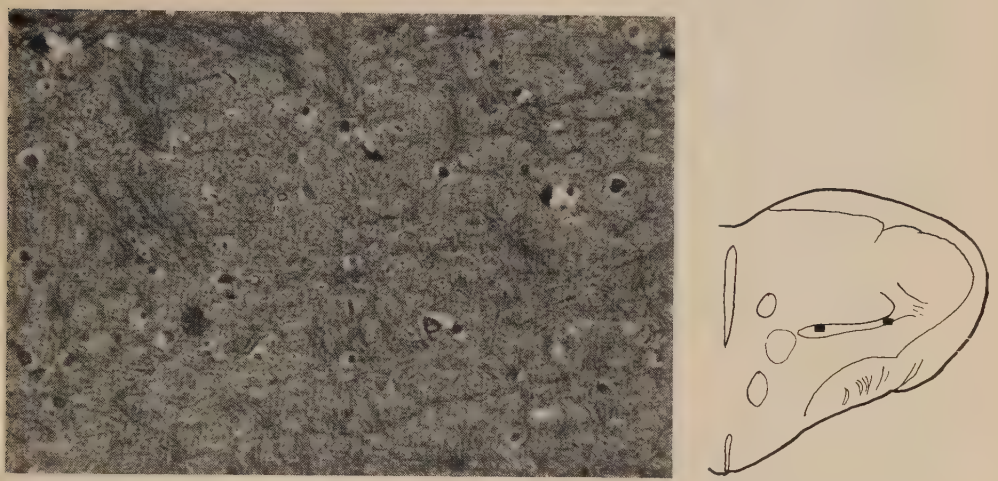


Fig. 20. The thin fibres are taking their site in the medial part of the V.M.L..

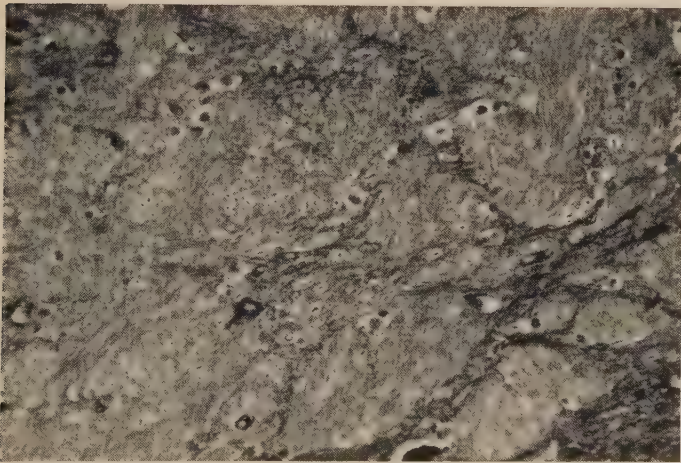


Fig. 21. The lateral part of the V.M.L. is occupied by the thick fibres.

6) EXPERIMENTAL MATERIAL.

a) *The posterior funiculi components.*

To study the medial lemniscus components originating in the nucleus gracilis, nucleus cuneatus internus and nucleus cuneatus externus, a series of lesions are made in this nuclear complex. The nomenclature used is that of H. MEESEN and J. OLSZEWSKI (1949), and the identity of the nuclei is controlled with a number of hemichordotomies on different levels. Rabbit H 3767 with a hemichordotomy at the level of L 5, H 3774 at Th 8, H 3765 at C 4 and H 3766 at C 1 are used. These four lesions give the information about the extension of the posterior funiculi nuclei. As described by LIU (1956) and MEHLER, FEFERMAN and NAUTA (1960), the fibres of the posterior funiculi originating in the cervical cord, proved to terminate in the Nc cuneatus externus. In accordance with MEESEN and OLSZEWSKI, from caudal to rostral the Nc gracilis and Nc cuneatus internus together are found at the lowest medullary level. They extend rostrally up to the caudal level of the inferior olive and there lateral to the Nc cuneatus internus, the Nc cuneatus externus begins to appear. From the mid- to the upper-olivary level only the Nc cuneatus externus is present, plotted between the ramus descendens of the trigeminal nerve and the restiform body (fig. 24).

A general view of the course of the M.L. could only be obtained by massive degenerations of its fibres; therefore in three rabbits, H 4535, H 4510 and H 4511 the M.L. itself was lesioned. In the first the lesion lies at the rostral level of the inferior olive, in the second at the level of the nucleus of the 7th nerve and in the third the rostral level of the trapezoid body. All the series rostral to the lesion are stained with Häggqvist and caudal to it with Nissl's staining method. A compact degeneration of the fibres in the M.L. is clearly visible in all three lesions. In the two lower, the degenerated fibres fill up the whole M.L. area rostral to the inferior olive and all the fibre bundles at the level of the trapezoid body. At levels rostral to the trapezoid body, the degenerated fibres shift to lateral and in the medial part masses of thin normal fibres join the M.L.. The fibres in the lateral part reach the medial side of the lemniscus lateralis. At the levels of the pons the degenerated fibres intermingle with the normal ones in the intermedial part of the M.L.. In the mesencephalon the degenerated fibre-component of the M.L. lies

in a dorso-latero-ventral position relative to the thin normal fibres, and rostrally it moves to lateral and to dorsal, not in circumscribed bundles, but spreading out over a large area. In the ventral medullary lamina of the thalamus the degenerated fibres assemble in the lateral part and intermingle with the normal fibres in the intermedial part. The fibres that lay in the latero-ventral part of the M.L. in the mesencephalon at higher levels shift to the ventral medullary lamina of the thalamus, by way of the subthalamus. These massive degeneration cases, allow a good general view of the display of the fibres from medullary origin.

In a number of rabbits the different posterior funiculi nuclei are lesioned. H 5177 with a large lesion of all the three nuclei, is stained with the Nauta-Gygax silver method. The first degenerated fibres forming the contra-lateral M.L., are found at the caudal level of the inferior olive. The degenerated fibres lie within the olive itself as well as between the olive and the raphe in the medial part, and the olive and the pyramidal tract in the ventral part of the M.L.. There is no fibre-termination to be seen in the inferior olive. At the levels rostral to the olive the degeneration is present over the whole area and it can be seen especially clearly in the bundles passing through the trapezoid body. At levels rostral to the trapezoid body the degeneration shifts laterally and part of it follows the lateral lemniscus into the inferior colliculus (fig. 22). In the ventro-lateral part of the inferior colliculus



Fig. 22. H 5177. After a lesion of the Nc gracilis and Nc cuneatus internus, the Nauta-Gygax staining-method shows a distinct terminal degeneration in the crossed inferior colliculus.

termination is clearly visible. The remaining fibres follow their way rostrally intermingling with the thin-fibred component only in the intermedial part of the M.L.. In the mesencephalon the fibres originating in the posterior funiculi nuclei, take their site dorsally, laterally and ventrally to the normal fibres. From this level the fibres independent from each other shift to the ventral medullary lamina of the thalamus. Some fibres, however, keep their ventral position a little longer and shifting more rostrally in their course to the lamina, pass through the subthalamus. In the thalamus the fibres terminate in the nucleus ventro-postero-lateralis (Nc V.P.L.), but some fibres proceed straight dorsally to the nucleus ventro-lateralis (Nc V.L.), where the termination is clearly visible.

H 5273, also stained with the Nauta-Gygax method, has got a lesion in the Nc gracilis, the Nc cuneatus internus and the caudal part of the Nc cuneatus externus. In this series the same degeneration is present in the inferior colliculus and in the nucleus ventro-postero-lateralis of the thalamus (fig. 23), but no terminations are visible in the Nc V.L.. This

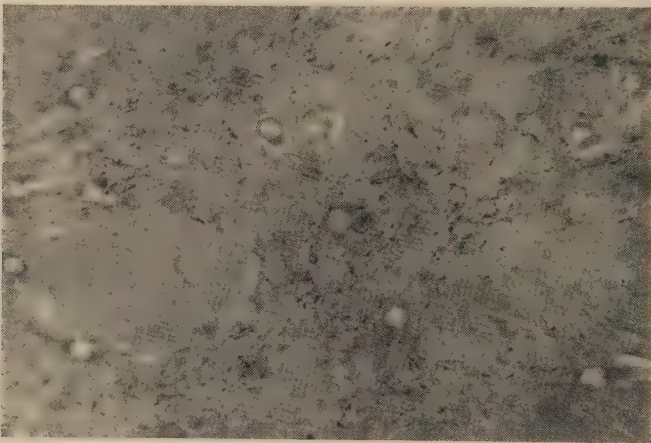


Fig. 23. H 5273. Terminal degeneration in the Nc V.P.L. of the thalamus after a lesion of the contralateral Nc cuneatus internus and cuneatus externus.

series substantiates the conviction that the fibres terminating in the inferior colliculus, originate in the nuclei gracilis and cuneatus internus.

To control the site in the M.L. of the fibres from the different nuclei, a number of animals with lesions of the posterior funiculi nuclei are

stained with the method of Häggqvist (fig. 24). In two animals, H 3770 and H 4505, at one side the Nc gracilis and at the other side both the Nc gracilis and Nc cuneatus internus are lesioned. In the M.L. contralateral to the lesion of the Nc gracilis only, the most caudal fibres



Fig. 24. A series of lesions of the posterior funiculi nuclei.

composing the M.L. are degenerated and pass through the inferior olive to take their site in the lateral part of the M.L. (fig. 25) between the olive and the pyramidal tract. At higher levels degeneration is present in the lateral part of the M.L. and to a smaller degree in the ventral part just dorsal to the pyramidal tract. In the M.L. contralateral to the lesion of the Nc gracilis and the Nc cuneatus internus, the degenerated fibres cover the lateral and more of the ventral part than at the other side (fig. 26). At the levels of the trapezoid body degenerated fibres from the Nc gracilis are found in the ventro-lateral bundles and those from the Nc gracilis and Nc cuneatus internus in

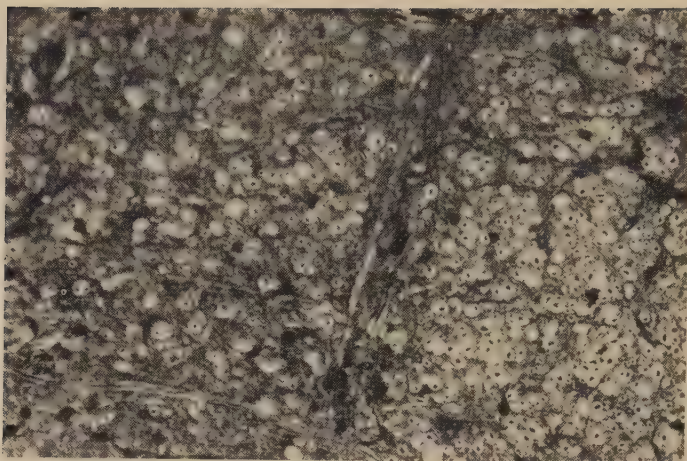


Fig. 25. H 3770, slide 63. The degeneration in the lateral part of the M.L. contra-lateral to the lesion of the Nc gracilis.

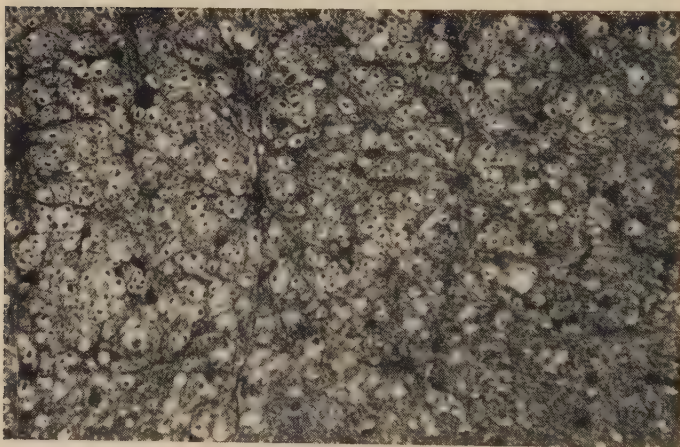


Fig. 26. H 3770, slide 63. The degeneration in the ventral part of the M.L. just dorsal to the pyramid. This is the lemniscus contra-lateral to the lesion of the Nc gracilis and Nc cuneatus internus.

the lateral part and in the whole thin-fibred ventral part. At the levels rostral to the trapezoid body, part of the degenerated fibres shift to lateral along the dorsal margin of the pyramidal tract and the dorsal pontine nuclei, to reach the lateral lemniscus. The fibres keeping their original medial position intermingle with the normal ones present, and from these levels on, as to the posterior funiculi nuclei fibres, no more lamination is present. The degenerated fibres mix also with the thin-fibred component reaching the M.L. in the caudal level of the pons. In the mesencephalon the degenerated fibres lie lateral, ventral and dorsal to the thin-fibred part of the M.L. and from these levels on we see the degenerated fibres move to lateral and to dorsal over a large area. In the ventral medullary lamina of the thalamus the fibres again group in a circumscribed area. In this lamina we see that the fibres of the Nc gracilis and Nc cuneatus internus take their site in the lateral part. In the Häggqvist preparations it is not possible to follow the degeneration shifting to the lateral lemniscus and to see it terminate.

Rabbit H 4504 with a lesion of both the Nc cuneatus internus and externus, shows a degeneration of the contra-lateral M.L. in the thin-fibred ventral part and in the dorsal part containing fibres of all sizes. At the level of the trapezoid body in the different bundles this is still very conspicuous. In the caudal part of the pons we see a small number of degenerated fibres shift laterally and meet the lateral lemniscus, they, however, cannot be followed further rostrally in the Häggqvist slides. The fibres in the medial position intermingle with the normal and thin-fibred component. In the mesencephalon the degenerated fibres lie latero-dorsal to the thin-fibred part and subsequently shift to the V.M.L. of the thalamus. In this lamina the degeneration is present in the lateral and also in the intermedial part.

Three animals with lesions only in the Nc cuneatus externus are H 3772, H 3769 and H 4503. In the contra-lateral M.L. the degeneration at the level of the rostral part of the inferior olive is found between the latter and the raphe. Above this level the degeneration takes its site in the dorsal part of the M.L. where fibres of all sizes, up to 10 micron, are present (fig. 27). At the rostral trapezoid level and in the caudal pons, the affected fibres intermingle with the normals but do not shift to lateral to reach the lateral lemniscus (fig. 28). In the mesencephalon they take a most dorso-lateral position relative to the thin fibres and intermingle somewhat with them. From these levels on the affected fibres, over a wide area shift dorsally and laterally to the V.M.L. of the thalamus. In this lamina they unite again in the intermedial part.

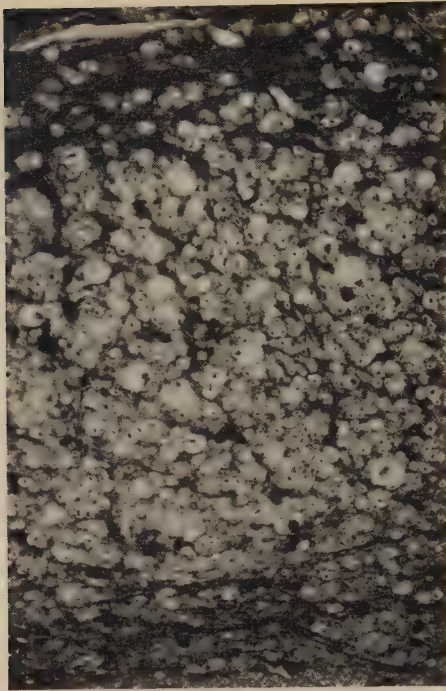


Fig. 27. H 3772, slide 299. In the M.L. contra-lateral to the lesioned Nc cuneatus externus, the degeneration is present in the dorsal part, at the level rostral to the inferior olive.

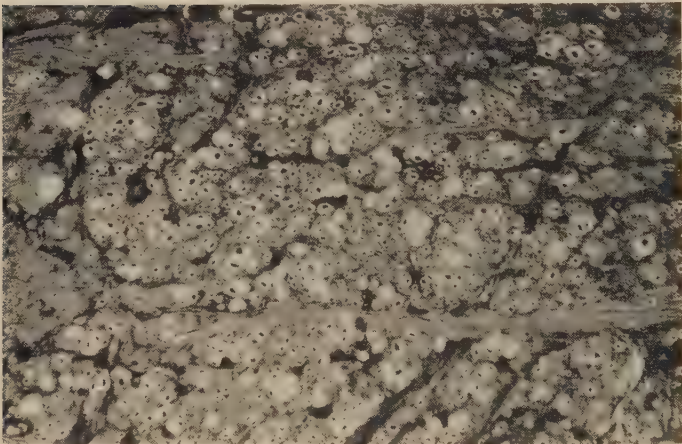


Fig. 28. H 3772, slide 217. At the mid-pontine level the degeneration takes its site lateral to the new thin-fibred component.

The third method to determine the origin of the fibres is the retrograde celldegeneration method. In the animals H 4535, H 4510 and H 4511 as we have seen, have been made a lesion in the M.L. itself. The brain stems caudal to the lesion have been stained with the Nissl method. As the animals have a survival time of 21 days no acute changes are present in the cells of the posterior funiculi nuclei. Comparing the nuclei of both sides it is evident, however, that contra-lateral to the lesion the number of cells is diminished. This is the case in all three nuclei, Nc gracilis, cuneatus internus and cuneatus externus.

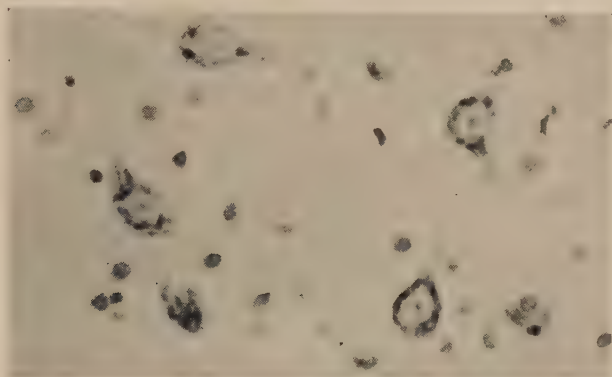


Fig. 29. H 5183, slide 13a. The normal aspect of the
Nc cuneatus externus.

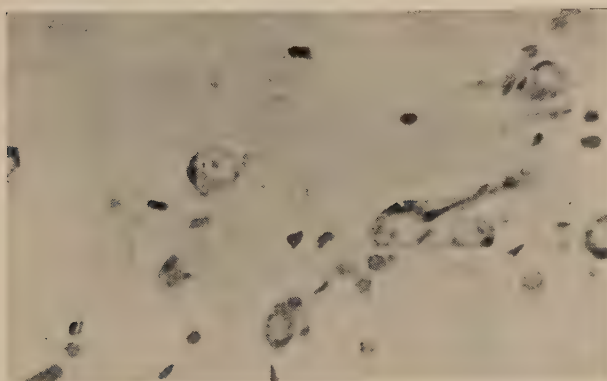


Fig. 30. H 5183, slide 13a. The Nc cuneatus externus
exhibiting retrograde celldegeneration after lesioning the
contra-lateral M.L..

Rabbit H 5183 presents a lesion of the M.L. at a mesencephalic level. The lesion covers the area with the thin-fibred component but has also damaged the thick fibres laying more dorso-laterally. In the Nissl-stained series we see that the cells of the Nc cuneatus externus show degenerative changes at the side contra-lateral to the lesion (fig. 29 and fig 30).

A series of animals with lesions of the M.L. has a survival time of 5 days. In these series (H 4801), stained with the method of Nissl, acute changes are clearly visible in the cells of the three posterior funiculi nuclei, contra-lateral to the lesion.

A view of the posterior funiculi nuclei fibres in the standard levels of the brain stem, is given in fig. 31.

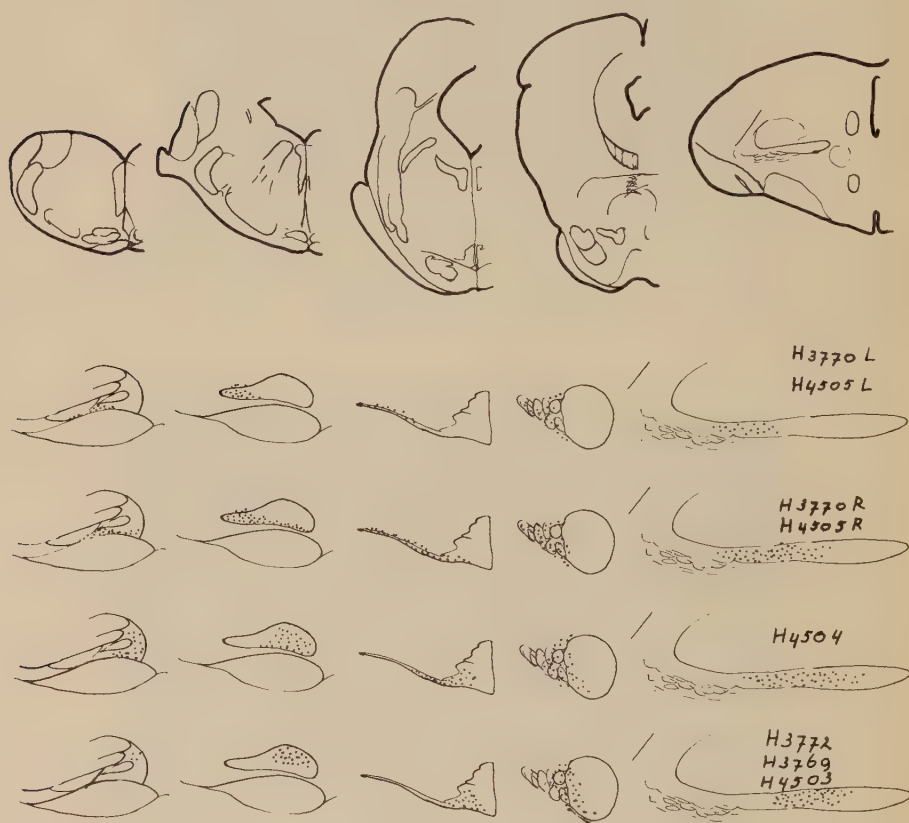


Fig. 31. The distribution of the posterior funiculi nuclei fibres in the M.L. and V.M.L. of the thalamus.

b) *The trigeminal component.*

To study the fibre-component from the trigeminal nuclei complex, a series of lesions are made all over the complex, the main nucleus as well as the descending branch nucleus. The nomenclature is that of MEESEN and OLSZEWSKI as used in their atlas of the rabbits brain stem. Most rostrally, besides the ramus mesencephalicus, we have the Nc sensibilis princeps Ne V, which caudally reaches to the level of the genu internum Ne VII. More caudally we find the Nc spinalis oralis Ne V, from rostral to caudal divided into three parts, γ , β and α . Subsequently caudal to the mid-olivary level the Nc caudalis spinalis begins, which reaches to the second cervical segment of the cord (fig. 32).

Two animals, H 4223 and H 3771, got a lesion of the Nc spinalis caudalis. The lesions do not touch the posterior funiculi nuclei and in both the series stained with Häggqvist's method, degeneration is present neither in the contra-lateral nor in the ipsi-lateral M.L..

H 3772 has got a huge lesion of the Nc spinalis oralis α overreaching somewhat upon the Nc spinalis oralis β . The passing electrode, however, lesioned the Nc cuneatus externus. In the contra-lateral M.L. we see only a small number of degenerated fibres about normal in quantity as to the small lesion of the Nc cuneatus externus, which take their site in the dorsal part. In regard to the small number and the place of these degenerated fibres, and taking in account the larger extent of the lesion in the Nc spinalis oralis, it is justified to consider them not of trigeminal origin.

Rabbit H 4140 is lesioned in the Nc spinalis oralis γ and a small rostral part of the Nc spinalis oralis β . The electrode has passed beyond the posterior funiculi nuclei, and only caused a lesion of the vestibular nuclei complex. The contra-lateral and the ipsi-lateral M.L. both are free of degeneration.

In four rabbits the main sensory nucleus is damaged, on guide of the stereotaxic atlas. In H 4137 the rostral part of the Nc spinalis oralis γ and the caudal part of the main nucleus are involved in the lesion. At the rostral level of the trapezoid body the first thin fibres reaching the M.L. of the contra-lateral side are degenerated. Somewhat more rostrally the thin fibres reaching the M.L. in the medial part are normal again and fill up the whole medial part. The degenerated fibres lie more laterally than the normal ones and intermingle with the thicker-fibred component. In the mesencephalon the affected fibres shift to dorsal and to lateral to reach the ventral medullary lamina of the thalamus. In this lamina the degenerated fibres are visible in the intermedial part

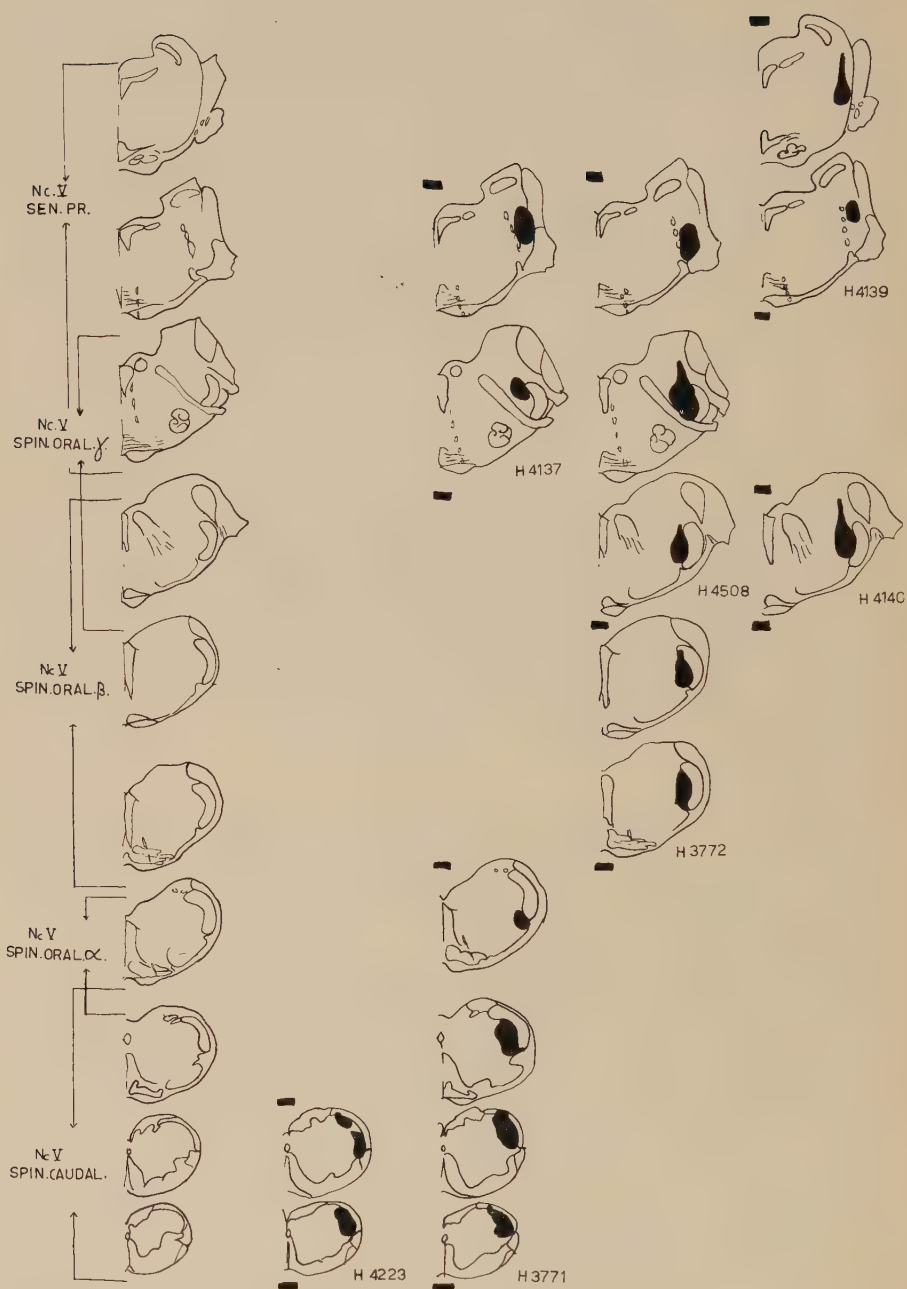


Fig. 32. A series of lesions of the trigeminal complex.

mixed with the normal ones, laterally the thick portion, medially the thin component.

Rabbit H 4508 has got a lesion involving the whole Nc princeps, except the most rostral part. Rostrally in the trapezoid body level the first fibres reaching the contra-lateral M.L. are degenerated (fig. 33). Subsequently over a fairly large distance all the fibres crossing the midline and reaching the M.L. show degeneration. The most rostral fibres reaching the lemniscus at the highest levels of the pons, however, are normal again. In the mesencephalon the whole thin-fibred part of the M.L. is degenerated. It is intermingled in the lateral part with normal thick fibres and in the medial part with normal thin fibres. At this level the fibres in bundles move to dorsal and to lateral over a wide area and reach the V.M.L. of the thalamus (fig. 34). Within this lamina the degeneration spreads all over its intermedial and medial parts.

Rabbit H 4139 with a lesion of the rostral end of the princeps nucleus, exhibits degeneration in the contra-lateral M.L. only in the higher levels of the pons and more rostrally. In their further course to the



Fig. 33. H 4508, slide 125. The first thin fibres joining the M.L. are degenerated after a lesion of the contra-lateral main sensory nucleus.

V.M.L., the affected fibres keep their medial position in the M.L. without intermingling with the normal thick-fibred component. In the mesencephalon the degenerated fibres move to dorsal and only a little to lateral, to reach the V.M.L. where they lie in the medial part.

Rabbit H 4138 is lesioned in the most rostral portion of the main nucleus. In the contra-lateral M.L. the fibres reaching them in the rostral pons and the caudal mesencephalon are degenerated. During the course rostrally they keep their dorso-medial position in the M.L. and after shifting dorsally to the V.M.L., we see them in the medial part of the lamina.



Fig. 34. H 4508, slide 83. The degenerated fibres shift laterally and dorsally to the V.M.L. of the thalamus.

The cells of origin of the trigeminal component of the lemniscus could be demonstrated with the retrograde celldegeneration method. In rabbit H 5183 the lesion covers the small-fibred part of the M.L. at the level of the caudal mesencephalon. In the series stained with Nissl's method we see degenerative changes only in the cells of the main sensory nucleus contra-lateral to the side of the lesion (fig. 35 and fig. 36). Neither in the oral nor in the caudal part of the spinal trigeminal complex degenerative changes are visible. In other rabbits exhibiting lesions of the M.L., retrograde celldegeneration is not conspicuous; possibly the animals used are too old to show changes in the small cells of the main sensory nucleus. In animals H 4535, H 4510 and H 4511, with lesions of the M.L. in the brain stem caudal to the thin-fibred component, changes are seen neither in the oralis nor in the spinalis caudalis nuclei of the descending trigeminal complex, while in the

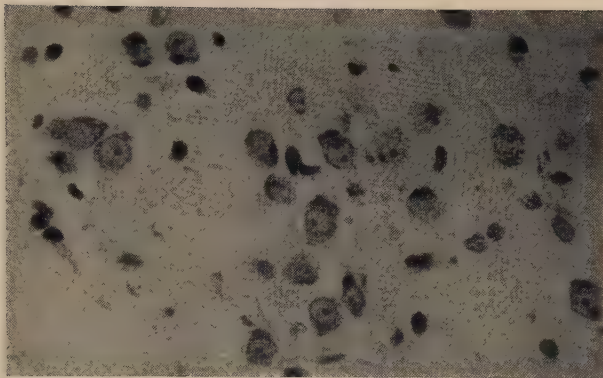


Fig. 35. H 5183, slide 9a. The normal aspect of the main sensory nucleus of the trigeminal nerve.

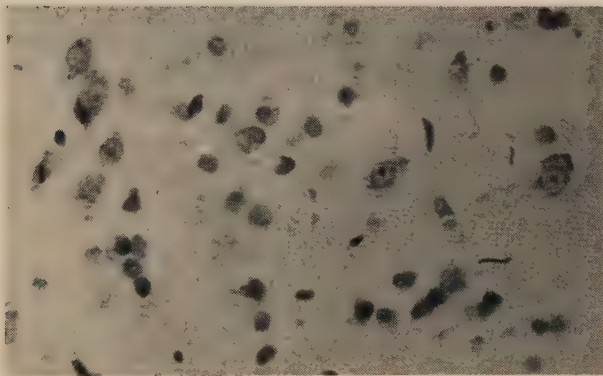


Fig. 36. H 5183, slide 9a. The degenerative changes in the main sensory nucleus after a lesion of the contralateral M.L.

posterior funiculi nuclei a decrease in the number of the cells is evident.

In the series H 4801 with a lesion of the M.L., acute changes are also visible only in the Nc princeps. The decrease of Nissl's substance and the removal of the cell nuclei from their central position is without doubt.

Fig. 37 represents the arrangement of the Nc princeps-fibres in the M.L..

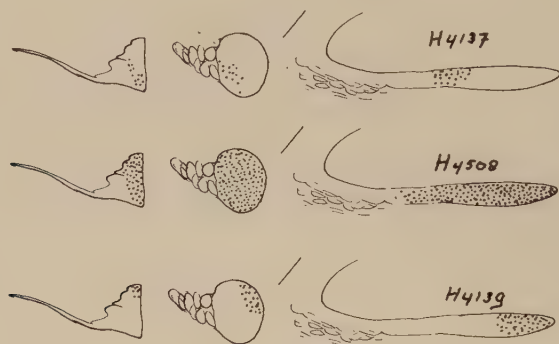


Fig. 37. The distribution of the trigeminal fibres in the M.L. and ventral medullary lamina.

c) *Fibres derived from the cervical cord.*

As mentioned in the survey of the literature, BUSCH in the cat and MATRICALI in the rabbit described a fibre tract lying ventral to the medial longitudinal fascicle in the cervical cord, that could be followed into the thalamus. This tract in the cat is called by VAN BEUSEKOM (1955) the cervico-olivary tract and by BUSCH the cervico-thalamic tract.

This small thin-fibred tract is clearly visible ventral to the M.L.F. in the two highest cervical segments. In rabbit H 3766 (hemichordotomy at C 1, Häggqvist stained) caudal to the lesion the normal thin fibres lie ventral to the degenerated M.L.F. (fig. 38). Rostral to the lesion the thin degenerated fibres take their site between the inferior olive and the pyramid. In higher levels they shift to the lateral part of the M.L., in this position subsequently running rostrally.

In three rabbits, H 5278, H 5279 and H 5280, at the level of C 1 this

fibre-tract is interrupted by an electro-coagulation lesion. In these animals (Häggqvist stained) the degenerated fibres lie in the lateral part of the M.L. between the inferior olive and the pyramidal tract, in which position they run rostrally (fig. 39 and fig. 40). At the pontine level the fibres take their site in the lateral spreading of the M.L. and subsequently possibly run to the medial geniculate body. The latter, however, cannot be verified in the Häggqvist-stained series. Degeneration of the cervico-thalamic tract in the caudal levels of the brain stem is not distinct in rabbit H 5347 (hemichordotomy at C 1, stained with the Nauta-Gygax method) because of many other degenerated systems lying in its neighbourhood. However, rostral to the level at which the

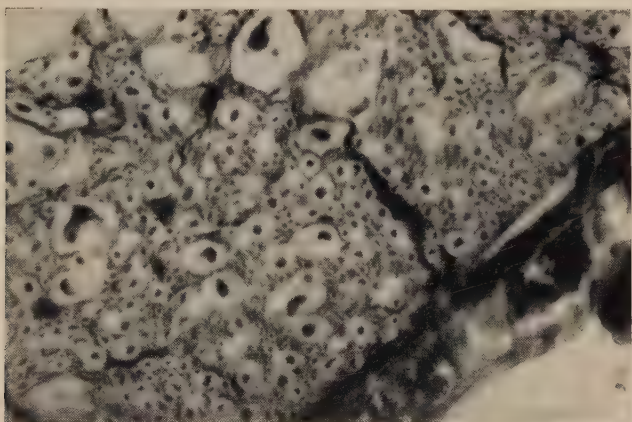


Fig. 38. H 3766. After a hemichordotomy at C1, the cervico-thalamic tract is clearly visible ventral to the degenerated M.L.F. 900 X

ventral spino-cerebellar tract turns to the superior cerebellar peduncle, the degeneration of the cervico-thalamic fibres is evident. Rostral to this level the degeneration can be found at the very lateral portion of the M.L., going to its termination in the medial geniculate body.

In the cat the cervico-thalamic tract originates in the Nc cervicalis lateralis as established by BUSCH (1957 and 1961) with retrograde degeneration. However, in our experiments with the method of retrograde celldegeneration its origin could not be determined because of the cells of the Nc cervicalis lateralis in the rabbit being widely spread and not

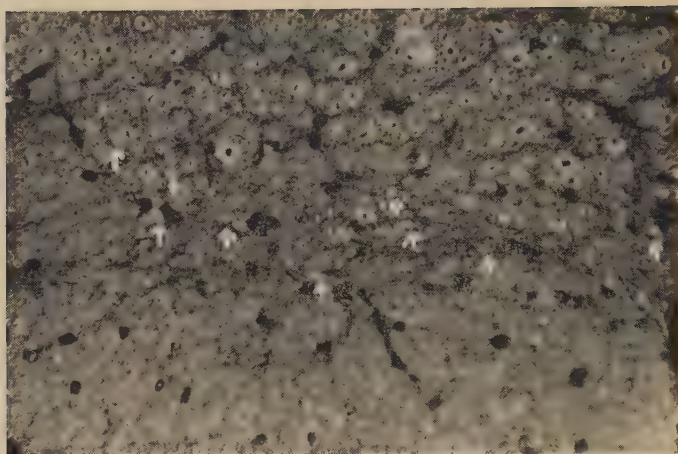


Fig. 39. H 5278, slide 3b. The cervico-thalamic fibres degenerated at the border-line of the pyramid and the M.L..

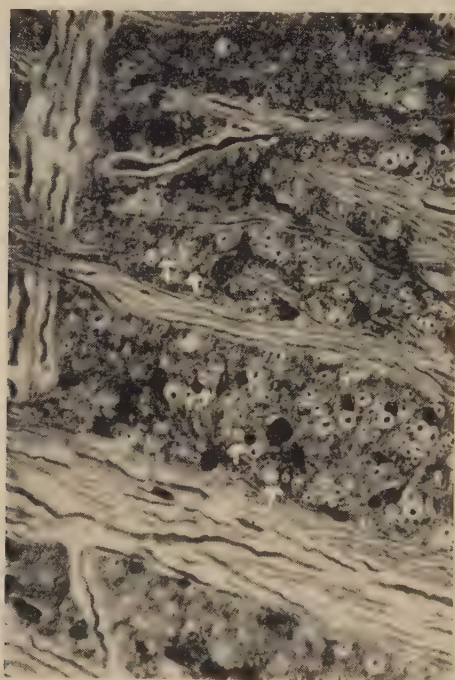


Fig. 40. H 5278, slide C. At the level of the trapezoid body, the cervico-thalamic fibres shift to the lateral part of the M.L..

forming a compact nucleus (fig. 41). In normal material of the rabbit it can be seen that the cervico-thalamic tract in the cord appears at the level of C 3, just rostral to the first wide-spread cells of the Nc cervicalis lateralis. These data may advocate the cervico-thalamic tract of the rabbit, originating in the Nc cervicalis lateralis as well.

The place taken by the cervico-thalamic fibres is shown in fig. 42.

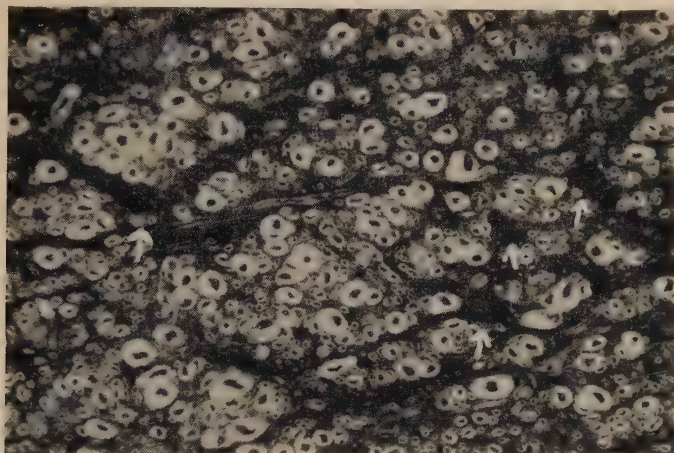


Fig. 41. The widespread cells of the Nc cervicalis lateralis at C2, just ventral to the posterior horn.



Fig. 42. Distribution of the cervico-thalamic fibres in the course of the M.L..

d) *Other components.*

In the literature other nuclear complexes are mentioned as origin of lemniscal fibres.

Lesions of the solitary tract nucleus and the vestibular complex did cause any degeneration neither in the contra-lateral nor in the ipsi-lateral M.L..

In the series with lesions of the M.L. and stained with Nissl's method also no changes are seen in the solitary tract nucleus or in other nuclei.

7) DISCUSSION.

As we have seen in normal material the fibre-composition of the M.L. from caudal to rostral changes considerably. The most caudal fibres constituting the M.L. appear at the caudal end of the inferior olive complex. In lesions of the contra-lateral Nc gracilis when degenerated they can be seen to shift laterally between the inferior olive and the pyramid. The fibres degenerating after a lesion of the contra-lateral Nc cuneatus internus lie in the ventral part of the M.L., medial to the fibres from the Nc gracilis. The fibres from the Nc cuneatus externus take their site in the most dorsal part of the M.L. between the olive and the raphe. These data are in accordance with the findings of VAN GEHUCHTEN (1903) in the rabbit, MATZKE (1949), GLEES et al. (1951), VERHAART (1954) and BUSCH (1961) in the cat and SIE PEK GIOK (1956) in man.

The fibres from the Nc cuneatus externus, which nucleus gets the cervical component of the posterior funiculi fibres, in the rabbit represent an important component of the M.L.. This is due to the large size of the nucleus as can be seen in the atlas of MEESEN and OLSZEWSKI and was verified by a series of hemichordotomies. They have been mentioned already by PROBST (1902) in the dog and by FERRARO and BARRERA (1936) in the monkey. In the present experiments it proved to be impossible to demonstrate the shift of fibres from the Nc cuneatus externus to the cerebellum, as frequently described.

This nucleus lies plotted between the restiform body and the descending branch of the trigeminal nucleus and therefore lesions of this nucleus always involve the margin of the restiform body.

At pontine levels the lamination of the M.L. gets less distinct and a number of fibres can be seen to shift laterally to join the lateral lemniscus in its medio-ventral part. These fibres are found only to be degenerated after lesions of the Nc gracilis and cuneatus internus. In Nauta-Gygax stained series we see them terminate in the inferior colliculus, as was already noted by WALLENBERG (1900) in the rabbit, and GEREBTZOFF (1939) in the cat, whereas SIE PEK GIOK in man saw a decrease of the M.L. fibres rostral to the superior colliculus level.

At rostral trapezoid and caudal pontine levels an enormous quantity of thin fibres joins the M.L. in its medial part and at more rostral

levels they constitute the bulk of the lemniscus. As already demonstrated they are exclusively derived from the contra-lateral main sensory trigeminal nucleus. Contrary to this statement WALLENBERG (1896 and 1905), PROBST (1902), WALKER (1939) and RUSSELL (1954) found fibres originating all over the trigeminal nuclei complex to join the M.L.. When studying their pictures of the lesions and the localisation of the fibres degenerated, however, it looks as if either the posterior funiculi nuclei, especially the Nc cuneatus externus, or the arcuate fibres were involved in the lesions intended to damage the nucleus of the descending trigeminus. In the present experiments described the lesions were placed very exactly on base of the stereotaxic atlas, and all the animals used were of the same breed. The trigeminal component of the M.L. being restricted to that of the main sensory nucleus is in accordance with the statement of VAN GEHUCHTEN (1901) in the rabbit and LEWANDOWSKY (1904) and BUSCH (1961) in the cat, although the latter leaves the possibility of a Nc interpolaris contingent open. Speculation about the nature of the main sensory trigeminus nucleus founded on being the only one projecting to the thalamus along the M.L. as yet are futile, the more so as the projection of the ramus descendens nucleus is unknown. In the rabbit where very precisely localized lesions can be made with the stereotaxic apparatus, this question may be more readily solvable than in other animals.

Similar to the posterior funiculi nuclei fibres, those of the princeps nucleus show a lateral- to medio-dorsal lamination within the M.L.. The fibres from the rostral part of the nucleus take their site in the medial portion, those from the caudal part in the lateral portion of the M.L., next to the thick-fibred component. At the caudal mesencephalon the fibres from the posterior funiculi nuclei are found dorsal, lateral as well as ventral to the thin-fibred trigeminal portion of the M.L., intermingling with them only at the borders. It is obvious that the latter fibres exceed the others enormously in quantity. This is in accordance with ROSE and MOUNTCASTLE (1960) stating that the projection area of the head in the thalamic nuclei exceeds that of the body tremendously in extent. Within the mesencephalon the thick fibres independent of each other spreading over a large area, shift dorsally and laterally to the ventral medullary lamina of the thalamus. In this lamina they assemble again and take their site in its lateral and intermediate parts. A tiny part of the thick fibres of the ventral portion of the M.L., in the mesencephalon do not take part in the dorso-lateral shift, but in their medio-ventral position proceed to the subthalamus and subsequently to the ventral medullary lamina of the thalamus.

This has been noted in the cat by MATZKE and BUSCH and in the macaca by BOWSHER. In Häggqvist-stained series we see the degenerated thick fibres proceed in the direction of the Nc V.P.L. of the thalamus. With the Nauta-Gygax method they can be followed to their termination in the Nc V.P.L. and we find a small number of them from the ventral medullary lamina run straight dorsally into the Nc V.L.. The termination in the Nc V.P.L. is in agreement with the findings of MATZKE and BOWSHER, whereas physiologically it has been confirmed by BERRY, KARL and HINSEY (1950) in the cat and by ROSE and MOUNTCASTLE (1952 and 1960) in the cat and the rabbit.

The numerous thin trigeminal fibres in the mesencephalon similarly shift dorsally and a little laterally into the V.M.L. of the thalamus, but they do not spread apart so much and keep much more their grouping in bundles. In Nauta-Gygax stained series their termination in the Nc V.M.L. is obvious, especially in the part known as the Nc arcuatus. This termination is substantiated by the experiments of MAGOUN and MCKINLEY (1942), MOUNTCASTLE and HENNEMAN (1952) and ROSE and MOUNTCASTLE. Especially conspicuous are the large number of trigeminal fibres and the large area of the Nc arcuatus they terminate in.

The third component of the M.L. originates in the cord. PROBST (1900) already mentioned it in the lateral part of the M.L. in the cat, and MORIN (1955) and CATALANO and LAMARCHE (1957) in the cat could demonstrate this pathway physiologically. VAN BEUSEKOM (1955) saw this tract in the cat's cord at cervical levels ventral to the medial longitudinal fascicle. BUSCH (1957) also in the cat recognized it as cervico-thalamic because of its origin in the cervical cord. MATRICALI described it in the rabbit on the base of anatomical experiments. By means of retrograde celldegeneration BUSCH was able to locate its origin in the Nc cervicalis lateralis. In the rabbit, however, this proved to be unfeasible because of the cells of this nucleus, being small and spread out over a large area, do not form a circumscribed nucleus. The course in the most lateral part of the M.L. and the termination in the medial geniculate body in the rabbit is similar to the cat. This can be demonstrated both with the Häggqvist because of the position it takes in the M.L. and the Nauta-Gygax method showing the termination.

8) SUMMARY.

In normal material, it is possible with Häggqvist's staining method, to recognize changes in the fibrepattern which may occur in the course of a tract. These changes were very clearly visible in the medial lemniscus of the rabbit. The first fibres composing the M.L. as such, at caudal olivary level lie between the olive, the raphe and the pyramid. Rostrally to this we see the M.L. covering an area along the raphe and being composed of three fibre-groups. In the ventral part there are fibres not surpassing 2 micron in diameter, in the lateral part fibres up to 5 micron in size and the whole dorsal part contains thicker fibres, some reaching the 10 micron diameter. At the rostral part of the trapezoid body, a large number of thin fibres, smaller than 2 micron, joins the lemniscus in its medial part. The original component shifts to lateral and at higher levels the whole medial part is formed by this new thin-fibred component. In the mesencephalon the thicker fibres are arranged around these thin fibres. From here these latter can be followed into the ventral medullary lamina of the thalamus, and shifting under the ventral nuclear complex this lamina rostrally decreases rapidly in size.

To analyze origin, course and termination of the different components three staining methods are employed: the Häggqvist and the Nauta-Gygax for degenerated fibres and the Nissl method for retrograde celldegeneration.

The posterior funiculi nuclei component originates in all three the nuclei: Nc gracilis, Nc cuneatus internus and externus. The fibres from these nuclei are arranged in the contra-lateral M.L. in the lateral part with fibres up to 5 micron, in the ventral layer with fibres up to 2 micron and in the whole dorsal part, where fibres up to 10 micron are present. This arrangement of the fibres is lost at pontine levels where all these fibres shift to lateral. Some of them from the Nc gracilis and Nc cuneatus internus reach the lemniscus lateralis and with it have their termination in the inferior colliculus. The remaining fibres from these nuclei and the fibres from the Nc cuneatus externus, in the mesencephalon, lie dorsal, lateral and ventral to the thin fibres and from here on they shift over a large area to the lateral part of the V.M.L. of the thalamus. The fibres ventral to the thin ones, reach this lamina by way of the subthalamus. All the fibres terminate in the Nc V.P.L. of the

thalamus, but after a lesion of the Nc cuneatus externus we also see a small number of fibres have their termination in the Nc V.L..

The thin-fibred component taking its site in the medial part of the M.L. at pontine levels, originates only in the Nc princeps of the trigeminal complex. Neither the pars oralis nor the pars spinalis proved to give fibres to the M.L., whereas lesions in the lemniscus itself did not cause retrograde celldegeneration in this nuclei. The caudal part of the Nc princeps provides the contra-lateral M.L. with its lateral thin fibres and the rostral part the medially located ones. This arrangement is maintained in the ventral medullary lamina of the thalamus. This large amount of fine trigeminal fibres has its termination in the Nc arcuatus of the thalamus, which in the rabbit is much larger than the Nc V.P.L. which is the nucleus of termination of the posterior funiculi nuclei component.

The third component of the M.L., consisting of fibres smaller than 2 micron, originates in the high-cervical medulla. The fibres in normal slides are already visible just caudal to the pyramidal decussation, where they lie ventral to the M.L.F. as a small tract of thin fibres. In the M.L. this component lies in a ventral and lateral position, but rostrally it shifts to lateral. The fibres terminate in the medial geniculate body. The origin in the Nc cervicalis lateralis could not be proved with retrograde celldegeneration, because the cells are widely spread over a large area, not forming a compact nucleus.

Fibres from other nuclei are not found in the M.L..

9) RIASSUNTO.

Nel materiale normale è possibile constatare con la colorazione di Häggqvist che nel decorso dei fasci del sistema nervoso si hanno cambiamenti nella ripartizione delle fibre di diverso calibro.

Nel coniglio è molto evidente la differenza nella composizione del lemnisco mediale a diversi livelli.

Le prime fibre che formano il lemnisco si trovano a livello della parte caudale dell'oliva inferiore, tra questa, la linea mediana ed il fascio piramidale. Anteriormente all'oliva il lemnisco copre un'aria situata medialmente e qui possiamo distinguere 3 gruppi di fibre a seconda del loro calibro. Nella parte ventrale vi sono fibre che arrivano fino a 2 micron, nella parte laterale fibre che arrivano fino a 5 micron ed in tutta la parte dorsale fibre che raggiungono i 10 micron di diametro.

A livello della parte anteriore del corpo trapezoide, numerose fibre di calibro inferiore a 2 micron si uniscono al lemnisco dalla parte mediale. Il componente originario si sposta lateralmente, per cui a livelli anteriori la parte mediale del lemnisco risulta formata dalle nuove fibre sottili. Nel mesencefalo le fibre originarie sono sparse attorno al nuovo componente di fibre sottili. Queste ultime fibre possono essere seguite fin nella lamina midollare ventrale del talamo; passando sotto il complesso nucleo ventrale del talamo si vede diminuire lo spessore di questa lamina.

Per individuare l'origine, il decorso e la terminazione di queste parti del lemnisco abbiamo impiegato tre metodi di colorazione: il metodo di Häggqvist e quello di Nauta-Gygax per le fibre degenerate ed il metodo di Nissl per la degenerazione retrograda dei nuclei.

Il componente proveniente dai nuclei dei fasci posteriori origina in tutti i tre nuclei, nel Nc gracilis, Nc cuneatus internus e Nc cuneatus externus. Nel lemnisco controlaterale si ha la seguente disposizione: nella parte laterale si trovano le fibre fino a 5 micron nella parte ventrale quello fino a 2 micron ed in tutta la parte dorsale le fibre fino a 10 micron di diametro. Questa ripartizione va perduta a livello del ponte, dove le fibre si spostano lateralmente.

Alcune fibre del Nc gracilis e del Nc cuneatus internus si uniscono al lemnisco laterale e terminano nel collicolo inferiore. Le rimanenti fibre di queste due nuclei e le fibre del Nc cuneatus externus si dispongono attorno alle fibre sottili del lemnisco su una estesa superficie, passando

così nella lamina medullaris ventralis del talamo. Le fibre situate ventralmente alle fibre sottili raggiungono la lamina medullaris attraverso un breve passaggio che percorre il subthalamo. Tutte le fibre che originano nei nuclei dei fasci posteriori terminano nel Nc V.P.L. del talamo ed alcune fibre provenienti dal Nc cuneatus externus anche nel Nc V.L..

Le fibre sottili che si uniscono al lemnisco anteriormente al corpo trapezoide provengono solo dal Nc principalis del trigemino contro-laterale. Né la pars oralis, né la pars spinalis del nucleo del trigemino cedono fibre al lemnisco; anche dopo lesioni del lemnisco non vi è degenerazione retrograda in questi nuclei. La parte caudale del Nc principalis del trigemino cede al lemnisco le fibre sottili laterali, la parte rostrale del nucleo cede le fibre del settore mediale. Questa ripartizione è ancora dimostrabile nella lamina medullaris ventralis. Tutte le fibre di origine trigeminale terminano nel Nc arcuatus del talamo, che copre una superficie molto più vasta del Nc V.P.L..

Il terzo componente del lemnisco è rappresentato da fibre di diametro inferiore a 2 micron, che originano nel midollo cervicale. Questo componente è molto distinto, anche nel materiale normale, subito caudalmente alla decussazione delle piramidi, come un sottile fascio situato ventralmente al fascio longitudinale ventrale. Anche nel lemnisco troviamo quest'ultimo componente situato nella parte ventrale e, procedendo rostralmente vediamo che esso si sposta in direzione laterale. Queste fibre terminano nel corpo genicolato mediale. Le loro origine nel Nc cervicale laterale non è stata dimostrata con la degenerazione retrograda poichè questo nucleo nel coniglio non è ben delimitato, ma è composto di cellule molto sparse.

Nel lemnisco non sono state trovate fibre provenienti da altri nuclei.

10) REFERENCES.

- ALLEN, W. F. *Formatio reticularis and reticulospinal tracts, their visceral functions and possible relationships to tonicity and clonic contraction.*
J. Wash. Acad. Sc. 22: 490-495, 1932.
- BECHTEREW, W. VON. *Ueber die Schleifenschicht.*
Arch. f. Anat. u. physiol. Anat. 379-395, 1895.
- BERRY, C. M., KARL, R. C. and HINSEY, J. C. *Course of spinothalamic and medial lemniscal pathways in cat and rhesus monkey.*
J. of Neurophys. 13: 149-156, 1950.
- BERRY, C. M., ANDERSON, F. D. and BROOKS, D. C. *Ascending pathways of the trigeminal nerve in cat.*
J. of Neurophys., 19: 144-153, 1956.
- BEUSEKOM, G. T. VAN. *Fibre analysis of the anterior and lateral funiculi of the cord in the cat.*
Thesis, Leiden, Eduard IJdo N.V. Leiden, 1955.
- BIAGIO, F. DI, and GRUNDFEST, H. *Lateral cervical nucleus as site of final relay to inferior olive in cat.*
J. Neurophys. 19: 10-20, 1956.
- BOWSER, D. *Projection of the gracile and cuneate nuclei in macaca mulatta; an experimental degeneration study.*
J. Comp. Neurol., 91: 259-296, 1949.
- BÜRGI, S. und BUCHER, V. M. *Markhaltige Faserverbindungen im Hirnstamm der Katze.*
Monographien aus dem Gesamtgebiet der Neurologie und Psychiatrie 87: 86-98, 1960.
- BUSCH, H. F. M. *Les connexions entre la moelle épinière et le thalamus chez le chat.*
Schweiz. Arch. f. Psychiat. u. Neurol. 80: 305-307, 1957.
- BUSCH, H. F. M. *The anatomy of the white matter of the brain stem of the cat.*
Thesis, Leiden, 1961, Kon. van Gorcum & Comp. N.V. Assen.
- CATALANO, J. V. and LAMARCHE, G. *Central pathways for cutaneous impulses in the cat.*
Am. J. Physiol. 189: 141-144, 1957.
- FERRARO, A. and BARRERA, S. E. *Lamination of the medial lemniscus in macacus rhesus.*
J. Comp. Neurol., 64: 313-324, 1936.
- GEHUCHTEN, A. VAN. *Voies sensitives centrales. La voie centrale du trijumeau.*
Le Nevraxe, 3: 237-261, 1901.
- GEHUCHTEN, A. VAN. *La voie centrale des noyaux des cordons postérieurs ou voie centrale médullothalamique.*
Le Nevraxe, 4: 3-44, 1903.
- GEREBTZOFF, M. A. *Des voies centrales de la sensibilité et du goût et leurs terminations thalamiques.*
Cellule, 48: 91-146, 1939.

- GLEES, P., SOLER, J. and BAILY, R. A. Retrograde axonal changes of the de-afferented nucleus gracilis following mid-brain tractotomy.
J. Neurol. Neurosurg. Psychiat., 14: 281-286, 1951.
- GLEES, P. and SOLER, J. Fibre content of the posterior column and synaptic connections of the nucleus gracilis.
Ztschr. f. Zellforschung, 36: 381-400, 1951.
- HARRIS, G. W. The induction of ovulation in the rabbit by electrical stimulation of hypothalamo-hypophyseal mechanism.
Proc. Roy. Soc. B., 122: 374-394, 1937.
- LEWANDOWSKY, M. Untersuchungen über die Leitungsbahnen der Truncus Cerebri und ihren Zusammenhang mit denen der Medulla Spinalis und des Cortex Cerebri.
Fischer Verlag, Jena, 1904.
- MAGOUN, H. W. and MCKINLEY, W. A. The termination of ascending trigeminal and spinal tracts in the thalamus of the cat.
Amer. J. Physiol. 137: 409-417, 1942.
- MATRICALI, B. Fibre provenienti dal midollo spinale nel bulbo e mesencefalo studiate nel coniglio con il metodo di Häggqvist.
Atti della Soc. It. Anat. (Monit. Zool. It.) Suppl. LXVI: 427-431, 1957.
- MATZKE, A. Course of fibres arising from nucleus gracilis and cuneatus of the cat.
Anat. Rec. 103: 487, 1949.
- MATZKE, A. The course of the fibres arising from the nucleus gracilis and cuneatus of the cat.
J. Comp. Neurol. 94: 439-452, 1951.
- MEESEN, H. and OLSZEWSKI, J. A cytoarchitectonic atlas of the rhombencephalon of the rabbit.
S. Karger, Basel-New York, 1949.
- MEHLER, R. W., FEFERMAN, M. E. and NAUTA, W. J. H. Ascending degeneration following antero-lateral cordotomy. An experimental study in the monkey.
Brain, vol. 83: IV: 718-750, 1960.
- MORIN, F. A new spinal pathway of cutaneous impulses.
Am. J. Physiol. 183: 245-252, 1955.
- MOUNTCASTLE, V. B. and HENNEMAN, E. The representation of tactile sensibility in the thalamus of the monkey.
J. Comp. Neurol. 97: 409-439, 1952.
- NAUTA, W. J. H. and KUYPERS, H. G. J. M. Some ascending pathways in the brain stem reticular formation.
Ford Symposium, Reticular Formation of the Brain: 3-30, 1957.
- NAUTA, W. J. H. and GYGAX, P. A. Silver impregnation of degenerating axons in the C.N.S..
Stain Technology, 29: 91, 1954.
- OLSZEWSKI, J. On the anatomical and functional organisation of the spinal trigeminal nucleus.
J. Comp. Neurol., 92: 401-409, 1950.

- PROBST, M. Experimentelle Untersuchungen über die Anatomie und Physiologie der Leitungsbahnen des Gehirnstammes.
Arch. f. Anat. u. Physiol. Anat. Suppl. 147-254, 1902.
- PROBST, M. Experimentelle Untersuchungen über die Schleifenendigung, die Haubenbahnen, das dorsale Längsbündel und die hintere Commissur.
Arch. f. Psych. u. Nervenkr. 33: 1-57, 1900.
- REIL, J. C. Die vorderen Schenkel, das vordere Markseggel und die Schleife.
Reil's Arch. f. d. Physiol., 9: 505-514, 1809.
- ROSE, J. E. and MOUNTCASTLE, V. B. The thalamic tactile region in rabbit and cat.
J. Comp. Neurol. 97: 441, 1952.
- ROSE, J. E. and MOUNTCASTLE, V. B. Touch and kinesthesia. Handbook of physiology and neurophysiology, Chapter XVII: 396-409, 1959.
- RUSSELL, G. V. The dorsal trigemino-thalamic tract in the cat, reconsidered as a lateral reticulo-thalamic system of connections.
J. Comp. Neurol., 101: 237-264, 1954.
- SAWYER, C. H., EVERETT, J. W. and GREEN, J. D. The rabbit diencephalon in stereotaxic coordinates.
J. Comp. Neurol., 101: 801-825, 1954.
- SIE PEK GIOK. Localization of fibre systems within the white matter of the medulla oblongata and the cervical cord in man.
Thesis, Leiden, Eduard Ydo, N.V. Leiden, 1956.
- TSCHERMAK, A. Ueber den centralen Verlauf der aufsteigenden Hinterstrangbahnen und den Beziehungen zu den Bahnen im Vorderseitenstrang.
Arch. Anat. Physiol. Lpz. Anat.: 291-402, 1898.
- VERHAART, W. J. C. Localisation of the medial lemniscus in the medulla and the pons.
Folia Psych. Neurol. Neurochirg. Neerl., 58: 35-41, 1954.
- VERHAART, W. J. C. L'analyse des cordons antérieurs et latéraux de la moelle épinière en rapport avec la structure du bulbe.
Comp. Rend. de l'assoc. des Anat. 92 b: 1-44, 1957.
- VERHAART, W. J. C. The anatomy of sensibility; anatomical aspects of centripetal conduction systems in the C.N.S. concerned with sensibility.
Fol. Psychiat. Neurol. Neurochirg. Neerl. 62: 503-522, 1959.
- VERHAART, W. J. C. Comparative aspects of the medial lemniscus.
Proceedings of the Second International Meeting of Neurobiologists. Amsterdam, 1959. Elsevier Publishing Comp. Amsterdam, 1960.
- VOOGD, J.
Thesis, Leiden. In print.
- WALKER, A. E. The origin, course and termination of the secondary pathways of the trigeminal nerve in primates.
J. Comp. Neurol. 71: 59-89, 1939.
- WALLENBERG, A. Die secundäre Bahn des sensibelen Trigeminus.
Anat. Anzeiger, 12: 95-110 und 474, 1896.

- WALLENBERG, A. Secundäre sensible Bahnen im Gehirnstamme des Kaninchens, ihre gegenseitige Lage und ihre Bedeutung für den Aufbau des Thalamus.
Anat. Anzeiger, 18: 81-105, 1900.
- WALLENBERG, A. Secundäre Bahnen aus dem frontalen sensiblen Trigemiuskerne des Kaninchens.
Anat. Anzeiger, 25: 145-155, 1905.

STELLINGEN

I

De vezels uit de nucleus van de tractus spinalis n. trigemini projecteren in de contra-laterale reticulaire substantie van de caudale pons.

II

Bij stoornissen in de bloed-liquor barrière, speciaal die, welke veroorzaakt worden door een infectie, dient de totale penicilline dosis de 1.000.000 E per 24 uur niet te overschrijden.

III

Door zijn eenvoudige techniek reeds, verdient de peritoneaal-dialyse de voorkeur boven de kunstnier.

IV

Bij jonge dieren ziet men in het C.Z.S. een snelle retrograde celdegeneratie optreden na traumatische beschadiging van de zenuwvezel. Dit verschijnsel is in tegenstelling tot het gedrag van andere weefsels, die juist zeer resistent zijn tegen beschadigingen.

V

De pars infundibularis van de adeno-hypophyse wordt eveneens geïnnerveerd door zenuwvezels afkomstig uit de pars caudalis tuberis. Deze vezels, die de neurohypophyse niet binnendringen, behoren niet tot de tractus hypothalamo-hypophyseos.

VI

De encephalitis post-vaccinalis berust op een allergische reactie.

VII

Neusverwijdende operaties bij klachten veroorzaakt door chronische rhinitis (vasomotoria) zijn zonder voorafgaand allergisch onderzoek niet verantwoord.

VIII

Indien men de bewegingsmogelijkheid van een gewricht, waarin in twee richtingen bewegingen kunnen plaats vinden, wil aangeven, verdient de term „twee graden van vrijheid” de voorkeur boven die van „twee-assig gewricht”.

IX

De RAI-TNO keuring voor veiligheidsriemen is geen garantie voor de doelmatigheid van de riem, maar uitsluitend een materiaal-controle. De keuring van de toegepaste modellen moet primair zijn.

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